



Canadian Special Publication of
Fisheries and Aquatic Sciences 103



N.A. Sloan and Paul A. Breen

Northern Abalone,
Haliotis kamtschatkana
in British Columbia:

Fisheries and Synopsis of
Life History Information

89-02251/

**Northern abalone,
Haliotis kamtschatkana,
in British Columbia:
Fisheries and synopsis of
life history information**

N. A. Sloan¹

*Department of Fisheries and Oceans
Fisheries Research Branch
Pacific Biological Station
Nanaimo, British Columbia, Canada
V9R 5K6*

and Paul A. Breen

*Ministry of Agriculture and Fisheries
Fisheries Research Centre, Box 297
Wellington 6003, New Zealand*

**Scientific Excellence
Resource Protection & Conservation
Benefits for Canadians**

**DEPARTMENT OF FISHERIES AND OCEANS
Ottawa 1988**

¹ Present address: 3249 W. 49th Ave., Vancouver, B.C. V6N 3T5.



Published by

Fisheries
and Oceans

Communications
Directorate

Publié par

Pêches
et Océans

Direction générale
des communications

Ottawa K1A 0E6

©Minister of Supply and Services Canada 1988

Available from authorized bookstore agents, other bookstores
or you may send your prepaid order to the
Canadian Government Publishing Centre
Supply and Services Canada, Ottawa, Ont. K1A 0S9

Make cheques or money orders payable in Canadian funds
to the Receiver General for Canada

A deposit copy of this publication is also available
for reference in public libraries across Canada.

DFO 4050
Cat. No. Fs 41-31/103 E
ISBN 0-660-12122-0
ISSN 0706-6481

Communications Directorate

Nicole Deschênes
John Camp
Gerald J. Neville

Director General
Director
Editorial and Publishing Services

Cover photo: R.M. Harbo

Correct citation for this publication:

SLOAN, N.A., AND P.A. BREEN. 1988. Northern abalone, *Haliotis kamtschatkana*,
in British Columbia: fisheries and synopsis of life history information. Can.
Spec. Publ. Fish. Aquat. Sci. 103: 46 p.

CONTENTS

Abstract / Résumé	iv	4.43 Growth	11
1. Introduction	1	4.44 Metabolism	14
2. Identity	1	4.45 Size and Age	15
2.1 Taxonomic Description	1	5. Population (Stock)	15
2.2 Nomenclature	1	5.1 Structure	15
2.3 Suprageneric Affinities	2	5.11 Sex Ratio	15
3. Distribution	2	5.12 Age Composition	15
3.1 Total area	2	5.13 Size Composition	15
3.2 Differential Distribution	2	5.2 Abundance (Density)	17
3.21 Spawn, larvae, and juveniles	2	5.21 Habitat-Related Variability and Total Abundance	17
3.22 Adults	4	5.22 CPUE as an Index of Abundance ..	18
3.3 Mobility	5	5.23 Density as an Index of Abundance ..	19
3.4 Hybridization	6	5.3 Recruitment	19
4. Bionomics and Life History	6	5.4 Mortality	20
4.1 Reproduction	6	6. Exploitation and Management	22
4.11 Sexuality	6	6.1 Introduction	22
4.12 Maturity	7	6.2 Non-Commercial Exploitation	22
4.13 Mating and Fertilization	7	6.21 Native Indian Fishery	22
4.14 Gametogenesis	7	6.22 Recreational Fishery	22
4.15 Fecundity	7	6.3 Commercial Fisheries	23
4.16 Spawning	7	6.31 History	23
4.2 Preadult History	8	6.32 Fishing Areas	24
4.21 Embryonic and larval phases	8	6.33 The Present Fishery	24
4.22 Post-Larval and juvenile phases ..	9	6.34 Commercial Fishery Management ..	28
4.3 Adult Phase	9	6.35 Stock Assessment	29
4.31 Longevity	9	6.36 Surveys	31
4.32 Hardiness	9	6.4 Changes in Abundance	32
4.33 Competitors	9	6.5 Transplantation for Improved Growth ..	37
4.34 Predators	10	7. Mariculture	38
4.35 Parasites and Diseases	10	8. Recommendations for Future Northern Abalone Research	40
4.36 Maximum Size	10	9. Acknowledgments	41
4.4 Nutrition and Growth	10	10. References	41
4.41 Food	10		
4.42 Feeding	11		

Abstract

SLOAN, N.A., AND P.A. BREEN. 1988. Northern abalone, *Haliotis kamtschatkana*, in British Columbia: fisheries and synopsis of life history information. Can. Spec. Publ. Fish. Aquat. Sci. 103: 46 p.

A comprehensive review of the life history and fisheries for the northern abalone, *Haliotis kamtschatkana* Jonas 1845, is presented with special emphasis on British Columbia populations. The literature on northern abalone throughout its range is discussed and compared with the literature on life histories of other *Haliotis* species worldwide. The exploitation (commercial/recreational/native) and management of northern abalone resources are described. The commercial northern abalone fishery is a minor one in British Columbia with populations fully exploited. There is some evidence that the a recent history of declining population abundance may be abating. Local commercial exploitation by divers expanded rapidly in the late 1970s (peaking at 433 t in 1978), but is now conducted at a much reduced level (quota of 47.2 t in 1987). Reasons for population decline are discussed and key gaps in life history data are identified. We conclude that the highest research priority for northern abalone should be to determine factors affecting recruitment.

Résumé

SLOAN, N.A., AND P.A. BREEN. 1988. Northern abalone, *Haliotis kamtschatkana*, in British Columbia: fisheries and synopsis of life history information. Can. Spec. Publ. Fish. Aquat. Sci. 103: 46 p.

Les auteurs présentent une revue exhaustive du cycle vital et de la pêche de l'orveau japonais, *Haliotis kamtschatkana* Jonas 1845 en mettant particulièrement l'accent sur les populations de la Colombie-Britannique. Ils discutent des ouvrages portant sur cet orveau dans toute son aire de dispersion et les comparent aux ouvrages sur le cycle vital d'autres espèces d'*Haliotis* partout dans le monde. Ils décrivent comment s'effectuent l'exploitation (commerciale/sportive/des autochtones) et la gestion des ressources d'orveau japonais. La pêche commerciale de cette espèce est une pêche de faible envergure en Colombie-Britannique car les populations y sont exploitées au maximum. Il y a des raisons de croire que la baisse récente de l'abondance des populations pourrait s'atténuer. L'exploitation commerciale au niveau local par les plongeurs a connu une expansion rapide à la fin des années 70 (atteignant un sommet de 433 t en 1978), mais elle se fait maintenant à un niveau très réduit (contingent de 47,2 t en 1987). Les auteurs discutent des causes de la baisse des populations et relèvent les principaux secteurs où il y a un manque de données sur le cycle vital. Ils concluent que les recherches sur l'orveau japonais devraient s'attacher en priorité à déterminer les facteurs qui influent sur le recrutement.

1. Introduction

Abalone, gastropods of the family Haliotidae (genus *Haliotis* Linnaeus, 1758), have long been fished in countries bordering the Pacific and the northeast Atlantic (Mottet 1978; Harrison 1986). Among the over 90 described species, most of which live in temperate and tropical seas, the northernmost species is *Haliotis kamtschatkana*, which occurs in British Columbia. The fisheries biology of the main commercial species worldwide has been reviewed by Mottet (1978). Most abalone fisheries have a history of high landings followed by decline (Stephenson 1924; Mottet 1978; Breen 1986; Harrison 1986).

In the western north Pacific there are ancient fisheries around Japan and the Koreas (Ino 1966). Along the North American coast in the eastern north Pacific, native exploitation has occurred for thousands of years. Artisanal fisheries began in the 1850's off California and in the early 1900's off British Columbia (Cox 1962; Quayle 1962; Tegner 1988). North American landings have generally declined after the advent of SCUBA and/or HOOKAH diving fisheries in the 1960's. In California eight species or subspecies of *Haliotis* occur (Cox 1962). *Haliotis rufescens* (red abalone), *H. corrugata* (pink), *H. cracherodii* (black), *H. fulgens* (green), and *H. sorenseni* (white) are harvested commercially or for recreation. *H. assimilis* (threaded), *H. walleensis* (flat), and *H. kamtschatkana* (pinto) occur but are rarely harvested commercially.

Only the "northern" or "pinto" abalone, *Haliotis kamtschatkana*, occurs in Washington State, British Columbia and Alaska waters. In British Columbia, northern abalone is a traditional food of native Indians, a popular recreational shellfish, and the target of a small commercial diving fishery. The commercial northern abalone fishery in British Columbia is a well documented invertebrate fishery with a detailed historical review by Federenko and Sprout (1982), other management-based reviews (Sprout 1983; Farlinger and Bates 1985; Jamieson 1986; Breen and O'Halloran 1987), stock assessments (Breen 1980b, 1986) and numerous surveys (section 6.36).

An unregulated fishery proceeded at a low level in British Columbia for many years. Landings increased sharply in the late 1970's, after which stocks declined and numerous management controls on harvesting were invoked. Much effort went into surveys and fishery data gathering. Now, a better understanding of fundamental life history characteristics of the species is needed.

Our purpose is to describe fully what is known about the life history of *H. kamtschatkana* in comparison with other *Haliotis* species, and to recount the history of local fishery and management practices. All available data have been brought together to aid future management considerations and provide a basis for recommending research directions. Excluding recent surveys, no new research results on northern abalone are presented here.

The format used here generally follows that of FAO species synopses and provides a framework for comprehensive life history and exploitation reviews. This is the first in a series of reviews of Pacific Canadian commercial invertebrates.

2. Identity

2.1 Taxonomic Description

McLean (1966) provides the following description for the northern abalone: "Shell relatively small, thin, elongate-oval, low. Open holes 3 to 6, on tubular projections. Broad channel present on body whorl between suture and row of holes. Sculpture of irregular lumps superimposed over spiral sculpture of broad ribs with weak spiral ribs in interspaces. Color mottled reddish or greenish with areas of white and blue. Shell margin narrow. Muscle scar lacking, interior pearly white with faint iridescence of pink and green." British Columbia specimens differ from California specimens in not having a broad channel in the body whorl, a less complex distribution of lumps on the spiral sculpture and the presence of a muscle scar on the interior of some shells (Jamieson in press). The first (anterior) one or two holes serve, with the underside of the shell margins, as water intakes and those remaining (posterior) are exhalant for mantle cavity water and excretory products (Voltzow 1983).

In California *H. kamtschatkana* are called 'pinto' abalone in keeping with the tradition of naming abalone according to their colour. In British Columbia the term 'northern' abalone is used as the species is the world's northernmost abalone.

2.2 Nomenclature

The valid name for the northern abalone is *Haliotis kamtschatkana* J. H. Jonas, 1845. The type specimen has been lost and the type locality of Unalaska Island in the Aleutian archipelago is in error as no abalone species occurs in the Aleutians (Cox 1962).

The taxonomic history of the species has been reviewed from the northwest Pacific by Ino (1953) and from the northeast Pacific by McLean (1966). The species was thought to occur in northern Japan until Ino (1951) proposed that the Japanese form was a subspecies of *H. discus* Reeve, 1846; which he named *H. discus hannai* Ino, 1953.

Various names for the northwest Pacific form (Ino 1953) are:

Middendorff, A. T., 1847: *H. kamtschatkana* J. H. Jonas, 1845.

Dunker, W., 1861: *H. gigantea* Chemnitz, 1788.

Schrenk, L. V., 1867: *H. gigantea* Chemnitz, 1788.

Lischke, 1869: *H. gigantea* Chemnitz, 1788.

Sowerby, G. B., 1887: *H. kamtschatkana* J. H. Jonas, 1845.

Tryon, J. R., 1890: *H. gigantea* Chemnitz, 1788.

Iwakawa, 1919 (in Ino 1953): *H. gigantea kamtschatkana* J. H. Jonas, 1845.

Dall, W. H., 1921: *H. kamtschatkana* J. H. Jonas, 1845. Takatsuki, S., 1927: *H. gigantea discus* L. A. Reeve, 1846.

Oldroyd, T. S., 1927: *H. kamtschatkana* J. H. Jonas, 1845.

Ino, T., 1953: *H. discus hannai* T. Ino, 1953.

In the northeast Pacific two subspecies are recognized by McLean (1966); the northern *H. kamtschatkana kamtschatkana* J. H. Jonas, 1845 and the southern *H. k. assimilis* W. H. Dall, 1878. The flat, rugose and elongate shell of this northern subspecies differs from the southern subspecies *H. k. assimilis* which is characterized by a higher, more rounded and less rugose shell (McLean 1966). Basic colour of shell and flesh as well as spiral shell sculpture is the same between subspecies. Generally, however, the two are now considered separate species (Kozloff 1983; Ricketts et al. 1985). *Haliotis k. assimilis* has hybridized with four other abalone species in the southern California area (section 3.4).

McLean (1966) lists the following synonymy for *H. k. kamtschatkana*:

Many authors until Cox, K. W., 1962: *H. kamtschatkana* J. H. Jonas, 1845.

Pilsbury, H. A., 1890: *H. gigantea* var. *kamtschatkana* J. H. Jonas 1945.

Habe, T. and Kosuge, S., 1964: *Nordotis kamtschatkana* (J. H. Jonas, 1845).

McLean (1966) lists the following synonymy for *H. k. assimilis*:

Many authors until Cox, K. W., 1962: *H. assimilis* W. H. Dall, 1878.

Habe, T. and Kosuge, S., 1964: *Nordotis assimilis* (W. H. Dall, 1878).

Bartsch, P., 1940: *H. aulaea* P. Bartsch, 1940.

Bartsch, P., 1940: *H. smithsoni* P. Bartsch, 1940.

2.3 Suprageneric Affinities

Phylum Mollusca

Class Gastropoda Cuvier, 1798

Subclass Prosobranchia Milne-Edwards, 1848

Order Archaeogastropoda Thiele, 1925

Superfamily Pleurotomariacea Swainson, 1815

Family Haliotidae Rafinesque, 1815

3. Distribution

3.1 Total Area

Haliotis kamtschatkana ranges from Icy Strait, at the northern tip of Sitka Island, Alaska ($\approx 58^{\circ}\text{N}$) (Paul and Paul 1981) to Baja California ($\approx 27.5^{\circ}\text{N}$) (McLean 1966). Northern abalone are patchily distributed throughout their range with an affinity for exposed and semi-exposed coasts. In its northern range, *H. kamtschatkana* occurs from the lower intertidal zone to at least 100 m depth, whereas in its southern range it is strictly subtidal with most individuals at 10 to 20 m depth (McLean 1966). In British Columbia the 100 m depth range is based on anecdotal information from a fisherman who found a northern abalone on his anchor retrieved from that depth. Most of the adult population is found at < 10 m depth.

3.2 Differential Distribution

3.2.1 Spawn, Larvae, and Juveniles

Male and female northern abalone aggregate at the highest point in their shallow subtidal area to broadcast their gametes simultaneously (Breen and Adkins 1980a; section 4.16). Spawning-related aggregations of some other abalone species are well known (Shepherd 1986a).

The fertilized eggs of northern abalone sink (G. Calderwood, pers. comm.), but hatch within days into phototactic, free-swimming larvae which rise in the water column and become available for potential transport in currents (Olsen 1984; Calderwood 1985; section 4.21). The planktonic phase of abalone species is generally short (Mottet 1978) and in northern abalone is reported to be 5 to 6 days (Olsen 1984). Quayle (1971) cites the short planktonic larval phase of *H. kamtschatkana* as responsible for the absence of larvae in monthly plankton samples in Clayoquot Sound on the west coast of Vancouver Island (Fig. 1). Northern abalone larval dispersal is, therefore, likely to be limited.

Juvenile northern abalone < 10 mm long are hard to find. None have been found in searches under sea urchin spine canopies or in *Macrocystis integrifolia* holdfasts. They are occasionally found under boulders. They occur mostly deeper than adults on smooth bedrock or boulders at 5 to 15 m depth (Breen 1980a). Such substrates are bare or covered with encrusting red coralline algae, but devoid of foliose algae.

Juvenile *Haliotis* spp. are widely reported to be associated with habitats characterized by crustose red algae (Saito 1981; Morse and Morse 1984; Prince and Ford 1985; Clavier and Richard 1986a). Settlement of *H. rufescens* larvae in California and their metamorphosis into benthic juveniles is evoked by chemical inducers present in crustose, geniculate and foliose red algae, but not green or brown macroalgae (Morse and Morse 1984). In particular, phycobilliproteins on the surface of crustose red algae (e.g. *Lithothamnium* spp. and *Lithophyllum* spp.), cyanobacteria and foliose red algae (e.g. *Porphyra* spp., *Laurencia* spp., *Gigartina* spp.) have been identified as settlement inducers in the laboratory (Morse and Morse 1984; Morse et al. 1984). Shepherd and Turner (1985) have demonstrated crustose coralline algal substrate selection through field experiments using *H. scalaris* and *H. laevigata* from South Australia, and Prince et al. (1987) reached the same conclusions for *H. rubra* in southern Tasmania. Saito (1981) reported that encroachment on encrusting red algae in Japanese waters decreased abalone nursery habitat.

Although species such as *Lithothamnium* have some ability to prevent settlement on their surface (Johnson and Mann 1986), red algal crusts are prone to becoming overgrown by fleshy algae or animals if not kept clean (Steneck 1986). Of the many possible sources of regular disturbance that could maintain the crust where *H. kamtschatkana* juveniles are found, herbivory by sea urchins (Pace 1981) and other grazers is paramount in importance. Morse and Morse (1984) suggest that the suite of grazers, including *Haliotis* juveniles, and the host encrusting algae exist in a mutualism. Grazers benefit the algae by main-

taining a clean surface; algae benefit the grazers by providing chemical cues for settlement, algal pigment which may make the small abalone shells cryptic, and a source of diatoms and micro-algal food. These authors suggest that the species have co-evolved, and that the chemical inducers function to maintain the relationship. In *H. discus hannai*, the mucous trails of conspecific and other adults may be an important cue to triggering settlement and metamorphosis (Seki and Kan-no 1981).

Juvenile northern abalone from ≈ 10 to 70 mm length have a weak tendency for cryptic habitats. Figure 2 shows that size frequencies of exposed northern abalone were larger than cryptic individuals collected from the same sites (Boutillier et al. 1985). Approximately 60 % of all abalone < 70 mm long were exposed and the percent exposure was uniform over the size range of 20 to 70 mm length. Those from 70 to 90 mm long were 90 % exposed and nearly all > 90 mm were exposed on rock surfaces. Juvenile *H. rufescens* are much more cryptic with

≈ 20 % of those < 90 mm being found exposed. They also tend to emerge to exposed surfaces as they grow (Tegner et al. 1988).

The observed change in habitat from exposed rock surfaces for very small juvenile northern abalone to cryptic habitats for some larger juveniles, and to exposure again for adults may result from changes in diet with size, and the effects of predation. Breen (1980a) proposed that very small juveniles graze benthic diatoms and microalgae, thus they need to live on exposed rock. Larger juveniles switch to feeding on drift macroalgae at night, taking shelter during the day. The cryptic habitat preferences of larger juvenile haliotids are well reported and usually related to shelter from predation (Mottet 1978; Shepherd and Turner 1985). The rates at which juvenile abalone become cryptic after settlement vary according to species (Shepherd and Turner 1985). Adult northern abalone experience less predation (section 4.34) and can occupy open rock continuously. Large adults

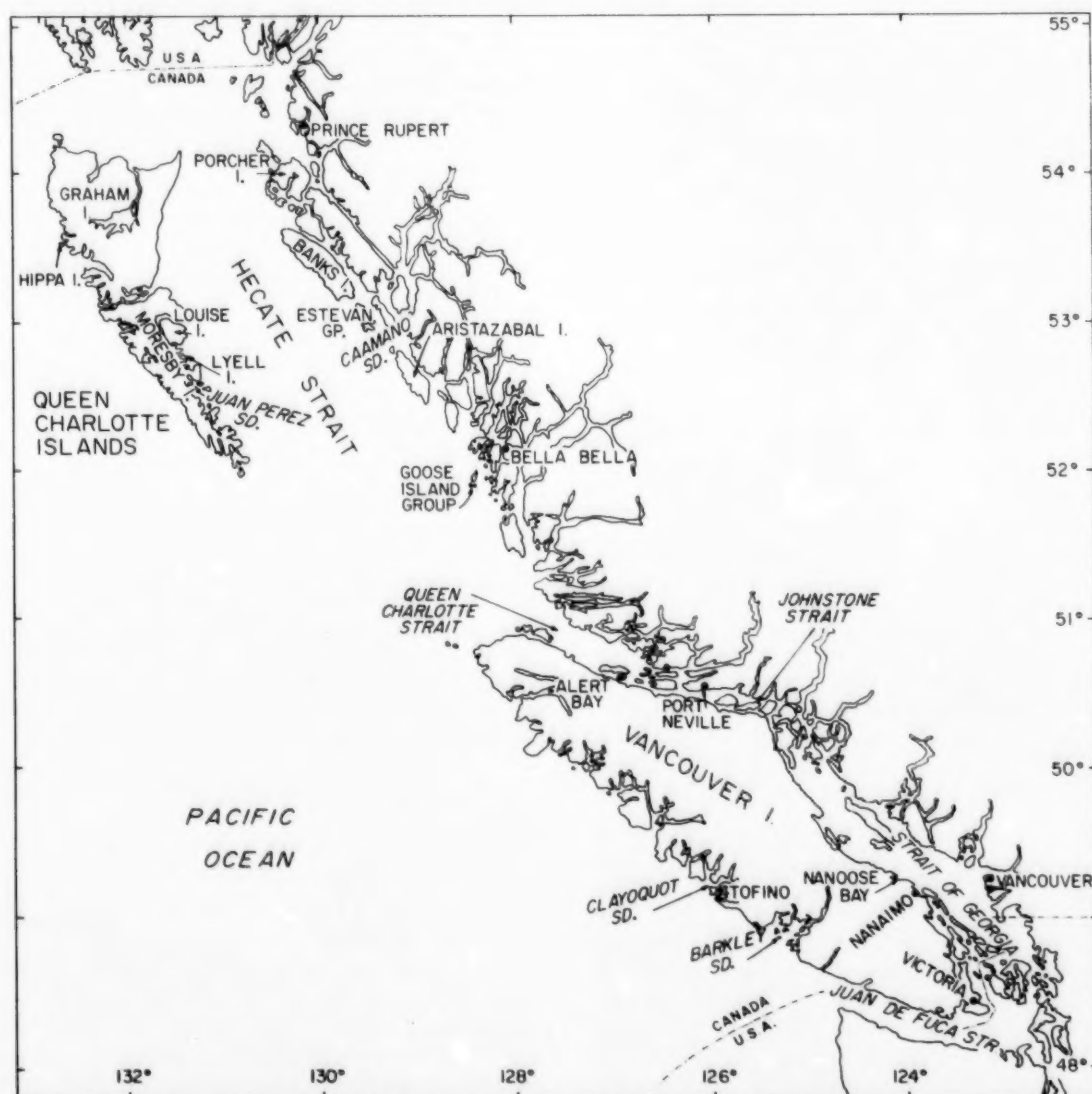


FIG. 1. The British Columbia coast showing the locations of *Haliotis kamschatkana* study and collection sites mentioned in the text.

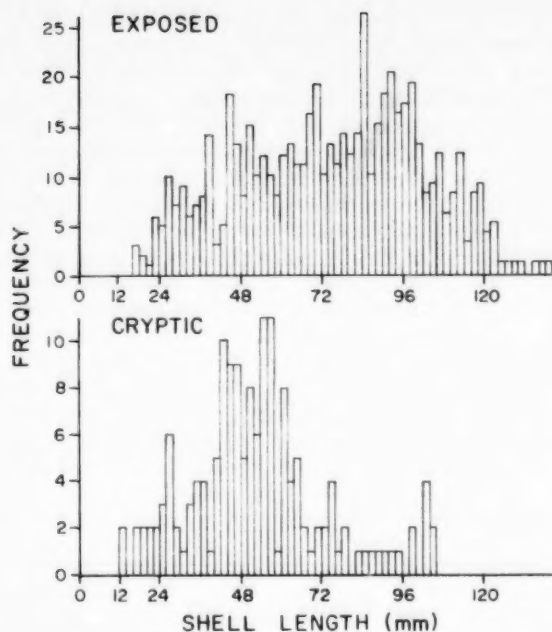


FIG. 2. Shell length frequencies of *Haliotis kamtschatkana* collected from exposed and cryptic rocky substrates on the east coast of Moresby Island, Queen Charlotte Islands (from Boutilier et al. 1985).

frequently show home scars, indicating that their movement is minimal and that feeding must be mainly on drift macro-algae. A similar pattern of ontogenetic behavioural change occurs in South African *H. midae*, which move from cryptic boulder habitats to exposed shallow reefs when they attain a shell length of >50 mm (Newman 1968), and in *H. rubra* from South Australia and Tasmania (Shepherd 1973a; Witherspoon 1975). *H. rufescens* at ≈ 50 mm shell length (≈ 1 year old) migrate from under boulders and between rocks into crevices where they capture drift kelp and experience shelter from predation (Hines and Pearse 1982).

In summary, the distribution of juvenile abalone is dependent upon healthy encrusting algal substrates. The resistance of this encrusting algae to epiphytic overgrowth mediated by the action of other grazers, such as sea urchins, chitons, limpets and perhaps adult abalone, aids in maintenance of abalone nursery habitat. Larger juvenile abalone may also benefit from protection provided by larger herbivores such as under the spine canopy of sea urchins (Kojima 1981; Tegner 1988).

In British Columbia, juvenile northern abalone are generally distributed deeper than adults (Breen and Adkins 1979, 1982). Figure 3 shows northern abalone size frequencies collected from a site in Juan Perez Sound, Queen Charlotte Islands. One sample was collected in the shallow *Pterygophora californica* forest, a second in the 10 m wide strip of sea urchin-dominated barrens immediately seaward of the kelp and a third in the deeper barrens. Nearly all 0+ and 1+ juveniles at this site were found in the barrens. This pattern could result from differential juvenile mortality between the deep and shallow zones, from differential settlement of juveniles,

followed by subsequent vertical migration, or a combination of these causes. Differential settlement seems probable because of the association between settlement and encrusting red algae, the primary rock covering in barrens, described above.

3.22 Adults

In British Columbia, northern abalone are widely but very irregularly distributed. Thomson (1914) stated: "This species is dispersed throughout the whole of the outer coast of British Columbia, including the west coast of Vancouver Island, but is not present in the Gulf of Georgia, as far as could be ascertained. It is never found in the inlets and the deeper sounds save at their mouths." They now occur in the inshore waters of the east coast of Vancouver Island, such as the Strait of Georgia although in relatively deep water, usually >7 m.

Outside Georgia Strait, northern abalone occupy a wide variety of habitats. They can be found directly exposed to the westerly swell, such as on the west coast of the Queen Charlotte Islands. They can also be found in still, quiet places. Between these extremes, they are found in many situations, and generalization is difficult.

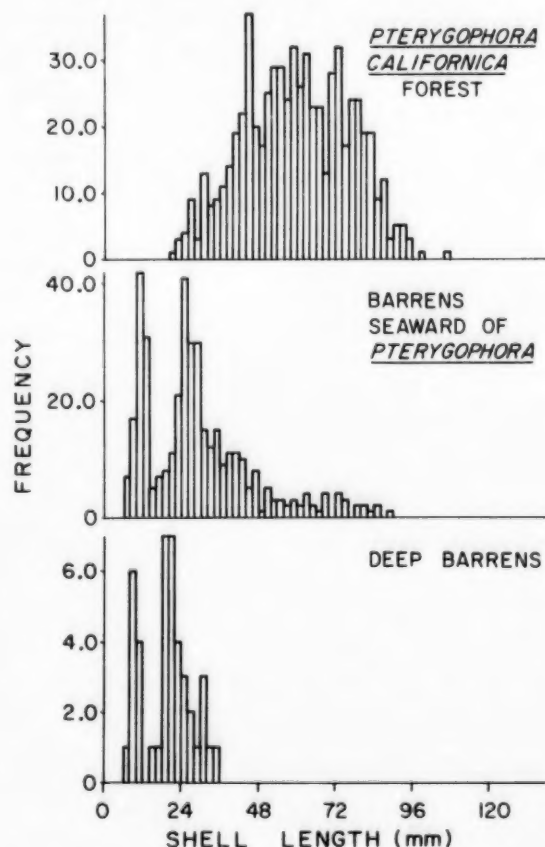


FIG. 3. Shell length frequencies of *Haliotis kamtschatkana* collected by stratified sampling from three depth zones at Hoskins Islet, Juan Perez Sound, Queen Charlotte Islands (from Breen and Adkins 1982).

They are capable of crossing sand or gravel, but usually require a firm substrate.

When density is measured in 1 m² quadrats, variance is always greater than the mean and increases with mean density, indicating a contagious distribution. The relation (Breen 1980b) is:

$$\ln \text{variance} = 0.428 + 1.54 (\ln \text{mean}).$$

Within the broad pattern of northern abalone distribution, their extreme patchiness makes it difficult to state inferences about factors affecting distribution. Moreover, commercial harvesting has altered distributions in many places.

The absence of northern abalone in long inlets and fjords, and the observation that individuals are found in deeper water in the Strait of Georgia, suggest that distribution may be limited by low-salinity water, seasonally high water temperatures, or both. The shallow waters of long inlets are strongly influenced by the rains of British Columbia's wet coastal climate (Thomson 1981) and by surface warming in the summer. Strait of Georgia surface waters are less saline than open coast waters and summer surface temperatures often exceed 20°C (Thomson 1981). Alaskan northern abalone die at 16 to 17°C (Paul and Paul 1981). Temperature tolerances might also explain changes in vertical distribution over the geographical range, with southern populations being found deeper than northern populations (McLean 1966). Other *Haliotis* spp. demonstrate differing distributions according to varied thermal tolerance ranges (Cox 1962; Leighton 1974; Shepherd 1975).

Northern abalone are absent from shallow water at extremely exposed sites. For example, on the exposed west shore of Hippa Island, Queen Charlotte Islands, the first abalone seen on the gently sloping bedrock only below ≈ 15 m depth whereas on the sheltered eastern shore they were seen at 3 m depth. In South Australia Shepherd (1975) found that some abalone species occurred at differing depths according to exposure while others tolerated direct wave action.

Although predation can influence the distribution of some abalone species (section 4.34), there is no evidence to suggest that it limits northern abalone distribution in British Columbia. Finally, northern abalone may be absent from some locations because no suitable juvenile habitat is present. Although the inshore rock substrate could be entirely suitable for adult abalone, lack of juvenile settlement might prevent their distribution.

From the differential distribution patterns of adult and juvenile northern abalone, we infer that settlement takes place in deeper water and that juveniles and adults migrate upward as they grow.

3.3 Mobility

Haliotis species generally move slowly, although there is considerable variability within and between species (Mottet 1978). They have a massive, muscular foot which functions as a complicated hydrostatic system in which differing muscles contract to generate pressure patterns that cause a range of specific body movements (Voltzow 1986).

Five specialized movement patterns have been observed in northern abalone: (1) they have a dramatic shell-twisting and running response from certain sea stars as described in section 4.34; (2) when removed from the substrate and placed on their shell, they can right themselves by curling an edge of the foot over to gain enough purchase to pull over on to their foot (Minchin 1975); (3) in currents they entrap drift algal fragments, as do *H. rufescens* (Cox 1962), by facing into the current, lifting the anterior half of the foot, and dropping the foot rapidly when they contact a fragment; (4) they can climb up kelp such as *Nereocystis luetkeana* and *Pterygophora californica* to graze on the plant, and when disturbed they retreat down along the kelp rather than drop off; (5) they elevate their shells during spawning as mentioned above in section 3.21. Observations on laboratory-held northern abalone and those made during night dives suggest that they are more active at night, although daytime activity is not uncommon.

In kelp forests, adult northern abalone can be relatively immobile if sufficient drift algal food is available (Breen 1980a). Large adult northern abalone frequently show home scars, indicating minimal movement and implying that feeding is mainly by entrapment of drift macro-algae (section 4.41). *H. tuberculata* off Brittany is another species whose mobility generally decreases with size and age (Clavier et Richard 1984). Quayle (1971) found that tagged northern abalone moved laterally < 50 m annually, and that little vertical movement occurred in the 0 - 10 m depth range. In a 1-yr study of ≈ 400 tagged individuals on the west coast of Vancouver Island, the greatest movement recorded was ≈ 20 m (P.A. Breen unpublished observation). Emmett and Jamieson (1988) recorded maximum movement of tagged northern abalone to be 125 m in one year. They concluded that little emigration of tagged abalone occurred outside placement sites overall. Tagging studies of abalone are confounded by the difficulty of detecting individuals which have moved significant distances over the usually complex terrain. Beinssen and Powell (1979) describe a technique for estimating abalone movement rates from repeated observations within a grid.

Mottet (1978) reviewed mobility in adult haliotids. Abalone may be stationary when an abundance of drift algal food is available (Poore 1972a; Shepherd 1973a) or may move an average 1.0 km annually (Newman 1966). Momma and Sato (1969) found that mobility in two coexisting species ranged between sedentary, mobile and homing (returning to the same starting point) with a maximum of 2.5 m covered in one night.

Shepherd (1986b) reported that movement in *H. laevigata* varied according to the amount of crevice space available. If suitable crevice space was available, animals were cryptic and sedentary; if crevice space was not available, then movement increased until shelter was located. Seasonal offshore movement occurred in intertidal *H. iris* from New Zealand during autumn and winter, probably to avoid storms, whereas subtidal populations tended to move much less. Moreover, coexisting *H. australis* showed no seasonal movements (Poore 1972a). An autumn seaward migration also occurs in Brittany *H. tuberculata* (Clavier et Richard 1984).

3.4 Hybridization

In British Columbia, no hybrids of *H. kamtschatkana* occur as it is the only species present. In northern Washington State, *H. kamtschatkana* and *H. rufescens* hybrids were seen a few years after transplantation of California *H. rufescens* (S. Olsen, Washington State Department of Fisheries, pers. comm.). Laboratory-reared hybrids of these species have been described from Washington State (Caldwell 1980).

The southern subspecies of the northern abalone, *H. kamtschatkana assimilis*, hybridizes with *H. rufescens*, *H. corrugata*, *H. sorenseni* and *H. wallalensis* in southern California (Owen et al. 1971). Commercial catch samples revealed 0.02–0.37 % of hybridization. In areas subjected to intense sea urchin grazing, frequency of hybrids could increase by an order of magnitude. Other possible reasons for hybridization were rarity of one parent species or extremities of range limits of one species. Species distinctions were suggested to be stable because of differing species' life histories, low hybrid larval viability and low affinity of heterospecific gametes (Owen et al. 1971). Talmage (1977) described and illustrated a naturally occurring hybrid of *H. rufescens* and *H. kamtschatkana* in California. Ino (1966) reported the common occurrence of natural hybrids of *H. discus hannai* (the Japanese species most similar to *H. kamtschatkana*) and *H. discus discus* in northern Japan. Hybridization is readily enough achieved in the laboratory to be considered as a technique for aquaculture or fisheries management (Leighton and Lewis 1982).

Haliotis species are amenable to genetic manipulation for enhancement of metamorphosis, juvenile development and growth (Morse 1984). Genetic cloning and amplification of recombinant-DNA templates for the production of essential growth-regulating hormones (insulin and growth hormone) has been achieved. These peptide hormones were taken up from external solution by *H. rufescens* larvae, resulting in improved food-conversion, assimilation, body growth and overall hardiness (Morse 1984).

4. Bionomics and Life History

4.1 Reproduction

4.1.1 Sexuality

Haliotis kamtschatkana, as all abalone species studied (Mottet 1978), is generally dioecious (Quayle 1971). Breen and Adkins (1982) found, based on gonad colour, that a "few" northern abalone were hermaphroditic. Olsen (1984) reported that in three separate instances, tagged captive male northern abalone demonstrated hermaphroditism. Two of the males kept for 12–15 months became females (verified by gonad colour change) by the second spawning season. The third male was observed to spawn eggs (immature and did not fertilize successfully) for 10 minutes, then change to sperm for 9 minutes. In three years of observations on captive females, none underwent sex changes.

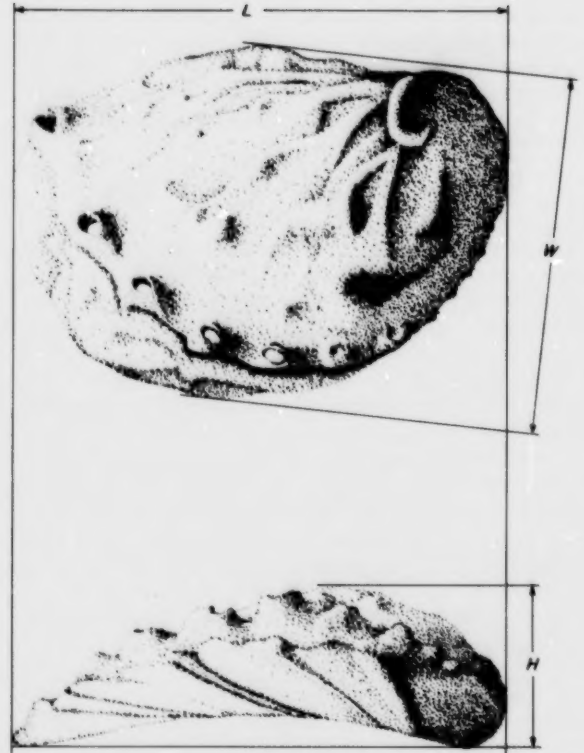


FIG. 4. Conventional *Haliotis* spp. shell measurements of length (L), width (W) and height (H).

When northern abalone are ripe, the sexes are easily discriminated by the dark green (female) or pink/beige (male) colour of their gonads. Gonads are visible by forcing down the epipodium on the right side (Quayle 1962). There is no sexual dimorphism of shell structure (McLean 1966). Breen and Adkins (1982) found no significant differences in shell morphometrics of male and female northern abalone at different localities (section 4.43). Conventional abalone shell measurements of shell length, width and height are illustrated in Fig. 4.

Sex ratios of northern abalone sometimes differ significantly from 1:1. Quayle (1972) found that 53 % of 2 914 individuals collected coastwide were males, a significant departure from 1:1 ($z=3.24$, $P<0.001$). Breen and Adkins (1982) reported the sex ratios of collections from three different depths at each of six different localities. Of 1959 northern abalone collected overall, 51.7 % were males, not a significant deviation from 1:1. A significant departure from 1:1 was observed at two sites: males were more abundant at one site and females at the other. To test whether differences in sex ratio might have been the result of protandric or progynic hermaphroditism, Breen and Adkins (1982) compared the mean lengths of males and females collected during population sampling. The means did not differ, which eliminates progandry and

progyny as a possible cause. Other species with a similar sex ratio of 1:1 are:

Species	Locality	Author(s)
<i>H. rufescens</i>	California	Young and DeMartini (1970)
<i>H. midae</i>	S. Africa	Newman (1967)
<i>H. tuberculata</i>	Guernsey	Hayashi (1980a)
<i>H. iris</i>	New Zealand	Poore (1973)
<i>H. australis</i>	New Zealand	Poore (1973)
<i>H. roei</i>	S. Australia	Shepherd and Laws (1974)
<i>H. cyclobates</i>	S. Australia	Shepherd and Laws (1974)

Shepherd and Laws (1974) found, however, that three other *Haliotis* spp. coexisting with the two above differed significantly with one being dominated by males among older individuals and the other two being dominated by females among adults. Shepherd and Laws (1974) stress the importance of sexing individuals at different size intervals, an often overlooked possibility.

The mechanism of sex determination in northern abalone is unknown. In *H. tuberculata*, Cochard (1980) suggested that individuals showed labile gonochorism. Sex determination had a strongly genetic base but may be influenced by environmental conditions.

4.12 Maturity

Quayle (1971) examined 816 histological preparations of northern abalone gonads and proposed that, in British Columbia, the sexes could be differentiated at ≈ 25 mm shell length and they become sexually mature at ≈ 50 mm shell length (≈ 3 years old). In southeast Alaska ($\approx 57^\circ\text{N}$), northern abalone mature at 66 to 75 mm shell length (Paul et al. 1977), later revised to ≈ 50 mm shell length (Paul and Paul 1981). In another Alaskan study from $55^\circ 30'\text{N}$, maturity occurred between 51 to 64 mm shell length (Larson and Blankenbeckler 1980).

4.13 Mating and Fertilization

Northern abalone, as with other *Haliotis* species, do not mate but broadcast gametes for external fertilization (Mottet 1978; Breen and Adkins 1980a).

4.14 Gametogenesis

Gametogenesis has been thoroughly described in numerous haliotids. Structure of gonads and the processes of gametogenesis are very similar (Quayle 1971; Mottet 1978).

Quayle (1971) examined histological preparations of northern abalone from different localities in British Columbia over several years. Ripe gonads were found throughout the year, although greatest occurrence of spent gonads was between April and June.

4.15 Fecundity

There are no published data on the fecundity of *H. kamtschatkana*. There is an unpublished estimate by S. Olsen (Washington State Dept. of Fisheries Shellfish Laboratory, pers. comm.) of 2.3 million eggs at 135 mm shell length. In an egg-per-recruit model, Breen (1986) used a curve of the form fitted by Poore (1973): $f = 0.0065 w - 0.098$ where f is fecundity in millions of eggs and w is whole weight in g. Because growth in northern abalone differs greatly in different habitats (section 4.43), it is likely that size-specific fecundity may also vary. Because of the importance of maintaining a minimum level of egg production (Sluczanowski 1984, 1986), fecundity and its variation require further study in northern abalone (sections 6.35 and 8).

Mottet (1978) proposed that haliotids are highly fecund and have a linear relationship between numbers of mature eggs in the ovary and body weight. The characteristically high fecundity of abalone may have evolved to offset environmental risk (Sluczanowski 1986). Poore (1973) reported that female *H. iris* 68 to 155 mm long produced 1 300 to 11.3 million eggs respectively and *H. australis* 62 to 91 mm long produced 46 000 to 2.9 million eggs, respectively. Similarly, Hayashi (1980a) showed that female *H. tuberculata* produced 38 000 eggs at 49 mm length and 5.1 million eggs at 115 mm length. Large female *H. midae* from South Africa can yield up to 25 million eggs (Newman 1967). Female *H. rufescens* produce ≈ 12.6 million eggs (Giorgi and DeMartini 1977), and the relation appears to be linear with body weight (Tegner et al. 1988).

Sainsbury (1982a) found that fecundity increased rapidly with size of *H. iris* from 100 to 1000 eggs at 70 mm shell length to ≈ 1 million eggs for abalone 120 mm long. After about 125 mm shell length, however, egg production decreased markedly with further increase in shell length. This may be an example of quantitative reproductive senility (Peterson 1983), in which older molluscs achieve less reproductive output than expected from the body size-reproductive productivity relationship (power curve) seen in younger adults.

4.16 Spawning

Northern abalone, as with haliotids generally, are synchronous spawners, and males and females broadcast their gametes (Mottet 1978; Breen and Adkins 1980a). Breen and Adkins (1980a) described a natural northern abalone spawning event in July from Lyell Island, Queen Charlotte Islands. Many of the spawners were stacked in piles of up to six in which only the bottom individual was attached to the rock. Individuals tended to go to the highest spot available, such as boulder tops and up kelp stipes, and raise their shells as high as possible. Females spawned with irregular strong puffs and males with more continuous emission. Shepherd (1986a) suggested that because of their increased vulnerability during spawning abalones should be protected during the spawning season.

The tendency for spawners to reach the highest point available to them is consistent with Quayle's (1971)

description of spawning in the laboratory. He observed northern abalone crawling to the top of the tanks and even falling out onto the floor. Ino (1966) observed that *H. discus hannai* moves into shallower water when spawning. These behaviours might act to increase fertilization rate in two ways. First, they could act to aggregate spawners in a local area, thus ensuring efficient fertilization. Second, they might increase the distance that eggs travel to the bottom, thus increasing their chance of encountering sperm.

Northern abalone in British Columbia can have ripe gonads year round, although Quayle (1971) found a peak in the proportion of post-spawned animals collected near Tofino in April through June. Emmett and Johnstone (1985) reported that gonad index was highest in summer (suggested June to August spawning) and decreased through the autumn and winter. They speculated that a "dribble type" spawning several times during the year was possible because males usually contained some active, mobile sperm and females contained some sufficiently developed eggs in November. In the laboratory spawning was in May at 9°C (Quayle 1971). In the field (52°38'N) Breen and Adkins (1980a) reported spawning in July. In Alaska Paul et al. (1977) reported spawning in the laboratory in June and July at 9°C and in southeast Alaska (= 55°30'N) Larson and Blankenbeckler (1980) suggested "mid summer" spawning occurred, although it apparently varied according to "general locations".

Spawning periodicity in haliotids ranges widely between species, and within species between localities and years (Poore 1973; Shepherd and Laws 1974; Mottet 1978; Hayashi 1980a, 1983; Shepherd et al. 1985). In some years an entire population will fail to breed (Poore 1973; Sainsbury 1982a). Spawning patterns vary between continuous, annual and biannual, in differing seasons according to species. This remarkable reproductive variability, even within species over relatively small areas, reflects local variability in physical and biological conditions (Shepherd and Laws 1974; Hayashi 1983). The massive foot functions as a nutrient reservoir for spawning (Hayashi 1983).

Temperature is a widely cited cue for spawning (Pearse 1978; Uki and Kikuchi 1984), but functions differently among abalone species. *H. tuberculata* spawns near maximum late summer temperatures (Hayashi 1980a), *H. rubra* spawns after summer maxima (Shepherd and Laws 1974), and *H. midae* spawning is associated with increasing temperature in some areas but not in others where more uniform temperatures accompany less episodic spawning (Newman 1967, 1969). Other factors influencing abalone spawning are: degree of maturation, intensity of stimuli, presence of gametes of conspecifics in ambient water, neural or hormonal factors, and availability of food (Shepherd and Laws 1974; Morse et al. 1977; Mottet 1978; Hayashi 1980a).

The most reliable methods for determining reproductive state are gonad index and oocyte size frequencies. The widely-used gonad index convention is described and illustrated by Hayashi (1980a). The sectioned conical portion of the visceral mass reveals the gonad sheathed in digestive gland. The relative proportions of these

visceral mass components indicates degree of gonad ripeness.

$$\text{gonad index} = \frac{\text{gonad area}}{\text{total area of cross-section}} \times 100.$$

Gonad indices are not useful for all species as Young and De Martini (1970) could not establish spawning time in *H. rufescens* using the index. Spawning is readily induced in the laboratory with a variety of stimuli well described in the extensive abalone mariculture literature (McCormick and Hahn 1983; Ebert and Houk 1984; Uki 1984).

4.2 Preadult History

4.2.1 Embryonic and larval phases

Aspects of the early life of northern abalone have been described from hatcheries by Beaudry (1983), Olsen (1984), and Calderwood (1985) (section 7). Within 48 h after fertilization, trochophore larvae emerge from their egg membranes. Rate of development is temperature-dependent, with the planktonic phase extending 4 to 8 days at 14 to 10°C, respectively. Larval development has not been described for northern abalone, but Calderwood (1985) suggests that it is likely to be very similar to that of *H. discus hannai* from northern Japan (Seki and Kan-no 1977).

The following is a generalized *Haliotis* early life history to the first few days of benthic life. There is considerable similarity in the early life history pattern of all abalone species (Mottet 1978).

Hatching of the heavier-than-water fertilized eggs releases phototrophic trochophore larvae which, at least in the laboratory, swim upward using their preoral ciliated ring or prototroch. Such behaviour could aid dispersal of the short-lived larvae. The non-feeding (lecithotrophic) larvae utilize stored yolk reserves until metamorphosis. By 40 h after fertilization, the first appearance of a larval shell and the conversion of the prototroch into a velum form veliger larvae which swim, but are no longer phototactic (Yano and Ogawa 1977). Within 3 days, the veligers have undergone torsion and can retract into their spiral shells, complete with operculum-like structures. Settlement usually occurs within another 11 days. In the first few days of the postlarval benthic phase, the velum remains intact and swimming is still possible. Feeding, using a toothed radula to rasp off benthic biota, begins immediately after settlement (Morse 1984; Morse and Morse 1984).

Tegner and Butler (1985a) demonstrated the importance of local current patterns in facilitating larval settlement of *H. fulgens* within a few kilometres of spawning sites in southern California. Forster et al. (1982) speculated that in cool summer waters (16–18°C), the planktonic period for *H. tuberculata* larvae could be prolonged to 5 or 6 days, during which time S.W. winds could transport larvae from Brittany to reseed abalone beds in the Channel Islands. Tanaka et al. (1986a, b) report that planktonic *H. discus hannai* larvae were collected by nearshore eddy currents in shallow rocky areas. They

reported more settlement on topographically complex "conglomerate" reefs orientated tangentially to the surf than smoother, more exposed vertical rock surfaces.

Leighton (1974) suggested that temperature may affect abalone larval survival: "survival of larvae dispersed in nature is likely dependent on their remaining within a water mass of appropriate temperature and further, settling in areas over which temperature change will not be extreme. Recruitment to marginal environments may rely on the timely influx of advanced veliger larvae".

Recently Prince et al. (1987) have proposed that *H. rubra* larvae may avoid planktonic dispersal altogether. They suggest that the heavy eggs are spawned at times of low water movement, sink to the bottom near the parental adults, hatch as demersal larvae and remain associated with cryptic rocky microhabitats in the immediate area as post-settlement juveniles.

4.22 Post-Larval and Juvenile Phases

In guts of hatchery-reared post-larval *H. kamtschatica*, minute benthic diatoms ($<10\ \mu\text{m}$) of the Order Pennales were found 2-6 days after settlement (Norman-Boudreau et al. 1986). Olsen (1984) also reported benthic grazing by northern abalone larvae on micro algae and bacteria soon after metamorphosis.

Section 3.21 recounts the importance of crustose coral-line red algae as a nursery substrate for recently-settled haliotids. Epiphytic benthic diatoms have been considered the most important food sources for young juveniles in culture (McCormick and Hahn 1983; Ebert and Houk 1984). In a detailed field study, Garland et al. (1985) showed that post-larval Tasmanian *H. rubra* feed on epiphytic bacteria (mostly *Moraxella* spp., which dominated the epibiota of the crustose algae; Lewis et al. 1985) and the crustose red algae itself. During light grazing juveniles rasped and ingested a layer 1-2 μm deep of algal cuticle and attached bacteria. During heavy grazing the deeper cytoplasmic contents of the epithallium underlying the cuticle were ingested (Garland et al. 1985). In 6 to 13 wk-old abalone, crustose algae dominated the juvenile's diets and bacteria found in their guts could have been functioning as gut symbionts rather than as food (Garland et al. 1985).

4.3 Adult Phase

4.31 Longevity

Maximum age of *H. kamtschatica* is unknown as there is no method for age determination (Fournier and Breen 1983). From growth curves (section 4.43), the largest abalone observed must be at least 15 yr of age. Breen (1980a) speculated that the large, extremely eroded shells, or those heavily riddled with the boring sponge *Cliona celata*, could be 50 yr old. Shells are also bored by the bivalve *Penitella conradi* (Morris et al. 1980).

Age determination in some *Haliotis* spp. by use of annual disturbance rings is well known (Mottet 1978). These rings are formed by cessation of somatic growth during gonad growth prior to spawning (Shepherd and Hearn 1983; Kim and Chung 1985), winter (Forster

1967; Poore 1972b; Kim and Chung 1985), or spring (Peng et al. 1984). Use of annual rings in estimating age and growth is reliable in *H. tuberculata* and verifiable by shell length frequency analysis and tag-recapture studies (Hayashi 1980b). Verification of annual rings in Japanese *H. discus discus* was reported by Kojima et al. (1977) and in Korean *H. diversicolor diversicolor* and *H. d. aquatilis* by Kim and Chung (1985). Rings in *H. iris* are currently being evaluated for age verification (T. Murray, New Zealand Ministry of Agriculture and Fisheries, personal communication).

Shepherd and Hearn (1983) stress that tag-recapture is the most reliable method for abalone growth studies and it can be further improved by *in situ* growth observations on caged animals. They caution that annual ring formation does not occur reliably in many haliotids. Furthermore, shell size frequency histograms may not be reliable unless reproduction is highly seasonal and growth rapid. In some abalone species growth ceases with age and old shells can be defaced by boring organisms such as the sponge *Cliona* (Hayashi 1980b) or by abrasion (M. J. Tegner, Scripps Institute of Oceanography, pers. comm.).

4.32 Hardiness

H. kamtschatica, as with other abalone species (Uki 1984), adapts well to captivity and can be maintained for long periods (Olsen 1984; Calderwood 1985).

4.33 Competitors

Competition between northern abalone and other species has not been examined experimentally, so any discussion of competition is speculative. The most obvious potential competitor for food and space with northern abalone is the red sea urchin, *Strongylocentrotus franciscanus*. Red sea urchins occur at mean densities from 1 to 10 m^{-2} at most sites where northern abalone are found. Similar to abalone, these sea urchins graze attached algae and entrap drift algae. Red sea urchins invaded sites where northern abalone harvesting occurred (Breen and Adkins 1979), and removed established kelp forest. The abundance of northern abalone is low at sites dominated by red sea urchins (section 5.13).

Vertical distributions of the two species are different, but overlap significantly. Red sea urchins have a characteristic sharp upper limit of distribution on shores with vertical relief. Above this point kelps grow; below this point sea urchins dominate barrens. The depth of this point varies with exposure to wave action and with temperature (Breen 1980c). Northern abalone are found both in the barrens and, as adults, in kelp forests above the vertical distribution of sea urchins.

In southeastern Australia, Shepherd (1973b) proposed that sea urchins invaded areas from which abalones had been removed, and that abalone harvesting changed the competitive balance of the two species. Japanese abalone growers believe that heavy sea urchin grazing can decrease abalone production (Uki 1984). In the only experimental examination of this topic, Tegner and Levin (1982) found that *H. rufescens* depressed the growth rate of *S. franciscanus* in the laboratory. They suggested that

abalone removals, along with other ecological changes (Tegner 1980), may have contributed to the increase in red sea urchin populations in California. A possible positive effect of red sea urchin grazing is the prevention of kelp overgrowth of encrusting red coralline algae, which is abalone settlement substrate (section 4.22).

H. rufescens and *S. franciscanus* interact in another way — the juveniles of *H. rufescens* use the spine canopy of red sea urchins as a habitat (Tegner and Levin 1982). There is no evidence for a similar relationship with northern abalone. In southern Japan sea urchins provide spine canopy shelter for out-planted juvenile abalone and significantly increase their survival (Kojima 1981).

4.34 Predators

Predation on juvenile northern abalone has not been observed. The highly cryptic behaviour of juveniles < 10 mm long (section 3.21) may relate to their susceptibility to predation. Octopuses, spiny lobsters (Tegner and Butler 1985b), crabs, predatory gastropods, and browsing fishes (Shepherd 1973a; Shepherd and Turner 1985) readily eat juveniles of other haliotids.

Predators of adult *Haliotis* species include sea otters (*Enhydra lutris*), fishes, sea stars, crabs and octopuses (Cox 1962; Shepherd 1973a; Mottet 1978; Hines and Pearse 1982). There are several predators of adult northern abalone in British Columbia waters. They are a minor component of the diet of *Octopus dofleini* (Hartwick et al. 1981) and they may be prey of browsing fishes such as the cabezon (*Scorpaenichthys marmoratus*), the wolf eel (*Anarrhichthys ocellatus*) and rock crabs (*Cancer productus*) (Emmett et al. 1988). The large sea star *Pcynopodia helianthoides* attacks adult northern abalone in aquaria and eats recently transplanted individuals in the field (Emmett et al. 1988). Unstressed adult northern abalone have an effective and rather specific escape response to *P. helianthoides*, similar to that reported from some California abalone species, of raising the shell and twisting it sharply from side to side (Montgomery 1967). As this takes place, the animal moves rapidly away from the point of contact with the sea star (section 3.3). On steep rock, the abalone sometimes loses contact with the substrate and falls, but this may be accidental. A *P. helianthoides* arm can be used to induce the escape response to collect abalones for tagging (Emmett et al. 1988). This method avoids damage to the foot which is common when abalones are pried off the substrate. Other defensive strategies of adult haliotids include powerful attachment to the substrate (Mottet 1978), permanent crevice occupation (Lowry and Pearse 1973) and shell configuration in older abalone that is complementary to the immediate substrate (Shepherd 1973a).

Sea otters are major abalone predators where they occur (Hines and Pearse 1982; Estes and VanBlaricom 1985). Sea otters in British Columbia appeared to be extinct after 1929 as a result of heavy exploitation for the fur trade in the nineteenth century (Cowan and Guiget 1965). Individuals from Alaska were introduced in 1969-72 (Bigg and MacAskie 1978), and have established two populations on the northwest coast of Vancouver Island. Abalones are rare and cryptic within the sea otter feeding range (Breen et al. 1982; Stewart

et al. 1982), but unfortunately no observations were made prior to the transplant. By analogy with observations in California (Lowry and Pearse 1973), it is possible that northern abalone were far less abundant on the British Columbia coast prior to sea otter hunting.

4.35 Parasites and Diseases

Mariculture of northern abalone in British Columbia has led to the discovery of a protozoan parasite (Phylum Labyrinthomorpha) lethal to virtually all infected hatchery-reared juveniles younger than 6 months old (Bower 1986, 1987a, b). Bower has described the parasite, its life cycle, pathogenicity and host specificity. Juveniles older than 6 months suffer $\approx 50\%$ mortality, by 1 year of age the majority do not succumb, and individuals 15 to 25 mm long cannot be infected.

H. rufescens in culture are susceptible to bacterial (*Vibrio*) infections (Elston and Lockwood 1983). Diseases and parasites of abalone in the wild are not well documented. A protozoan parasite (*Perkinsus* sp.) has been identified in *H. laevis* and *H. rubra*, and may be implicated in decreases of *H. laevis* in some parts of South Australia (Lester 1986; Lewis et al. 1987).

4.36 Maximum Size

Maximum size in a northern abalone specimen, collected near Victoria, B.C., is 165 mm shell length (Breen 1980a). There is another, unconfirmed, Victoria-area report of a specimen 175 mm long (D. B. Quayle, Pacific Biologic Biological Station, Nanaimo, pers. comm.). Maximum size appears to be smaller on the northern British Columbia coast. The largest specimen found by Quayle (1971) in 4 000 observations was 150 mm. Of more than 17 000 animals measured on the north coast from 1978 to 1984, only two were longer than 140 mm. The longest was 149 mm.

The largest abalone species is *H. rufescens*, with a maximum reported length of 280 mm (Cox 1962). *H. kamtschaticana* is the smallest of the eight abalone species found in California.

4.4 Nutrition and Growth

4.41 Food

The food of juvenile northern abalone, and juveniles of all other haliotids observed, is their nursery habitat substrate of encrusting coralline algae and its associated epibiota (sections 3.21, 4.21, 4.22).

As they grow, juvenile northeast Pacific abalone species do less grazing and assume the adult feeding preference for entrapment of drift algae over grazing attached algae (Cox 1962; Tegner 1988). Breen (1980a, b) suggested that drift brown algae were especially important food resources to northern abalone in British Columbia. Their approximate order of algal preference, was: *Macrocystis* / *Nereocystis* then *Laminaria*-*Pterygophora* (rejected in the presence of more preferred species)-*Agarum* (rejected outright) (P. Gee and J. Lee, Simon Fraser University, unpublished student reports). Breen (unpublished data) found that a group of small abalone consumed

Nereocystis at the highest rate, followed by *Macrocyctis*, *Laminaria saccharina*, *Costaria costata* and *Agarum*. Whether *Macrocyctis* or *Nereocystis* is the most preferred kelp remains unclear. The only published laboratory study on feeding revealed that Alaskan northern abalone will eat diatoms, brown, red and green algae and avoid certain species such as *Fucus distichus* and *Agarum cribrosum* (Paul et al. 1977).

In California, the mottled shell colour of northern abalone is suggested to represent relatively more benthic diatoms and coralline algae in their diets compared to larger coexisting species, such as *H. rufescens* and *H. corrugata*, which feed mostly on drift kelp (Cox 1962). In young haliotids the shell is readily marked by colour changes according to changes in the food eaten; in some cases dietary shifts lead to discrete banding (Olsen 1968). Young northern abalone fed *Nereocystis* grow light green shells (P.A. Breen, unpublished observation).

Diets in adult *Haliotis* vary considerably. For example, Australian and New Zealand species prefer red algae (Poore 1972c; Shepherd 1973b) whereas South African *H. midae* eat mostly brown algae (Newman 1969). In northeast Pacific abalone species, diets include diatoms, red and especially large brown algae (Cox 1962; Leighton and Boolootian 1963).

Diet can be influenced by the behaviour of abalone species. Poore (1972b) suggests that in some areas the relatively immobile *H. iris* are unselective, purely opportunistic, drift algal feeders; whereas coexisting *H. australis* are active foragers which graze attached algae or trap drift algae. In areas where drift algae are limited, *H. iris* can become an active grazer.

Although northern abalone can be found feeding directly on attached algae, their feeding activities appear to be unimportant to algal community structure. The removal of abalone from kelp forests by harvesting has had no obvious effect, although this has not been examined experimentally. Foster and Schiel (1985) state that *Haliotis* species have little effect on attached plants in California kelp forests.

4.42 Feeding

Young northern abalone feed by rasping the substrate with their radula for benthic diatoms and perhaps coralline algae with bacterial epibiota (section 4.22). At some

stage, young northern abalone switch preference to small pieces of drift algae and retain this as the primary feeding method thereafter (Breen 1980a). We have seen adult northern abalone feeding directly on the kelps *Macrocyctis integrifolia*, *Nereocystis luetkeana* and *Pterygophora californica*. Cox (1962) described the dexterity of *H. rufescens* in using their epipodia to grasp drift algae; this also applies to northern abalone (section 3.3). The amount of water movement transporting drift algal food to abalone at a particular site can be an important factor to local feeding characteristics (Shepherd 1973a; Sainsbury 1982a). It remains unknown to what extent adult haliotids switch between grazing and drift algal capture, but flexibility probably exists to exploit specific feeding opportunities.

4.43 Growth

Growth is well studied in haliotids. Growth can be described over a wide size range by the von Bertalanffy growth curve (Sainsbury 1982a), and is relatively slow (Harrison 1986). Growth is most often measured by the conventional shell dimensions illustrated in Fig. 4.

Growth in northern abalone has been examined in several ways. Growth checks on shells proved inconsistent and were abandoned in favour of tag-recapture studies. Table 1 lists the locations, dates and numbers of tagging in British Columbia. Quayle (1971) tagged $\approx 2\ 000$ individuals with numbered plastic discs or plastic spaghetti tags attached to the shell with monofilament nylon threaded through the oldest open respiratory pores. Later, Breen tagged 667 with numbered plastic discs bonded to the shell or strung through respiratory pores, and a further 4 100 with numbered plastic spaghetti tags strung through respiratory pores (Table 1). There was $\approx 5\%$ recovery of those released. Asymptotic length (L_{∞}) and the Brody coefficient (K), parameters of von Bertalanffy growth, were determined from data in Table 1 using Ford-Walford plots of lengths before and after recapture (Ricker 1975). The Brody coefficient was corrected to a value for 365 days (Table 2). L_{∞} varied from 95.2 to 137.3; K from 0.195 to 0.505. Extreme values of K were seen where recoveries were fewest.

Some of the variation in northern abalone growth rate can be explained by variation in habitat. Breen and

TABLE 1. Geographic co-ordinates, dates and numbers of *Haliotis kamtschatkana* marked and recovered in British Columbia growth studies reported from Quayle (1971) and Breen (1986).

Place	Lat. °N	Long. °W	Date released	Date recovered	No. released	No. legible recovered
Bauke Is.	48°51.9'	125°19.5'	25 Mar '64	10 Feb '65	—	31
Gilbert Is.	48°52.5'	125°19.6'	10 Feb '64	10 Feb '65	—	26
Sivart Is.	52°32.1'	131°35.6'	8 Jan '65	3 Feb '66	—	28
Ellis Is.	48°51.7'	125°06.4'	25 Oct '76	10 Nov '77	327	24
Bauke Is.	48°51.9'	125°19.5'	3 June '77	25 May '78	340	26
Lyell Is.	52°38.4'	131°27.3'	16 July '79	31 July '80	1500	13
Newberry Cove	52°28.1'	131°26.9'	17 July '79	2 Aug '80	1000	34
Hickey Is.	52°59.6'	129°31.6'	29 July '80	14 May '81	1100	94
Murchison Is.	52°35.7'	131°27.7'	1 Aug '81	10 July '82	617	62

TABLE 2. Estimates of the Brody coefficient (K) and asymptotic length (L_{∞}) in nine mark/recovery experiments on *Haliotis kamtschatkana* from British Columbia listed in Table 1. Values in parentheses are 95 % confidence limits (from Breen 1986).

Place	K	L_{∞} (mm)	Habitat / Type
Bauke Is.	0.317 (0.103-0.580)	123.7 (118.8-128.5)	<i>Nereocystis</i>
Gilbert Is.	0.204 (0.074-0.353)	137.3 (133.5-141.1)	<i>Nereocystis</i>
Sivart Is.	0.230 (0.128-0.346)	129.8 (126.8-132.9)	Not known
Ellis Is.	0.158 (0.00-0.434)	122.6 (116.1-129.1)	<i>Nereocystis</i>
Bauke Is.	0.351 (0.234-0.483)	114.2 (111.0-117.4)	<i>Nereocystis</i>
Lyell Is.	0.505 (0.366-0.668)	100.6 (98.2-103.0)	<i>Nereocystis</i>
Newberry Cove	0.195 (0.144-0.249)	95.2 (94.6-95.9)	<i>Pterygophora</i>
Hickey Is.	0.241 (0.129-0.365)	113.8 (112.0-115.6)	<i>Nereocystis</i> / <i>Pterygophora</i>
Murchison Is.	0.267 (0.07-0.510)	124.2 (116.3-132.2)	<i>Macrocystis</i>

TABLE 3. Parameters of the von Bertalanffy growth estimates for various *Haliotis* species.

Author	Species	Brody growth coefficient K	Asymptotic shell length L_{∞} (mm)
Poore (1972b)	<i>H. iris</i>	0.31	146
	<i>H. australis</i>	0.32	87
	<i>H. virginea</i>	0.32-0.44	61.5-64.4
Sainsbury (1982a)	<i>H. iris</i>	0.16	132
Shepherd and Hearn (1983)	<i>H. rubra</i>	0.32-0.34	143-144
	<i>H. laevigata</i>	0.48-0.59	138-148
Harrison and Grant (1971)	<i>H. rubra</i>	0.22-0.24	160-175
Newman (1968)	<i>H. midiae</i>	0.06	193*
Hayashi (1980b)	<i>H. tuberculata</i>	0.33-0.45	98-115
Clavier and Richard (1985)	<i>H. tuberculata</i>	0.37	108
Kojima et al. (1977)	<i>H. discus discus</i>	0.22-0.27	167-188
Haaker (pers. comm.)	<i>H. rufescens</i>	0.27	201

* Shell breadth

Adkins (1979) suggested that abalone in protected or semi-exposed locations with high-quality food, such as *Macrocystis* and *Nereocystis* forests, grew faster and to a larger size than those in exposed places with low quality food, such as *Pterygophora* forests. This hypothesis was developed to explain differences in population structure observed in different habitats (section 5.13). Food quantity and water motion should also be considered. *Macrocystis* produces large amounts of drift whereas *Pterygophora* produces very little (M. J. Tegner, Scripps Institution of Oceanography, pers. comm.). Moreover, *Pterygophora* occurs on more exposed substrates and the drift capture efficiency of abalone decreases in rough water (Shepherd 1973a). Abalone tagged in *Nereocystis* forests (Table 1) grew faster than those in *Pterygophora* forests. Growth of tagged and recaptured northern abalone from different kelp forest communities is illustrated in Fig. 5.

When northern abalone were transplanted from a *Pterygophora* habitat to a nearby *Macrocystis* forest their growth increased. Growth parameters at Hoskins Islet, a *Pterygophora* habitat, were estimated by Fournier and Breen (1983) to be $L_{\infty} = 92$ mm, $K = 0.20$. After one year, abalone transplanted to Murchison Island, a *Macrocystis* habitat, showed $L_{\infty} = 124$ mm, $K = 0.27$ (Table 3). Results are illustrated in Fig. 6. A similar increase ($L_{\infty} = 104$ to 133 mm, $K = 0.15$ to 0.33) was observed by Emmett et al. (1988), who transferred abalone from exposed *Nereocystis* and *Pterygophora* forests to more sheltered *Macrocystis* forests in Barkley Sound (section 6.5).

Quayle (1971) reported morphometric relationships among shell length and shell height, shell width, shell weight, total weight, meat weight in northern abalone. Breen and Adkins (1982) also examined morphometrics of total weight and various shell dimensions, finding no

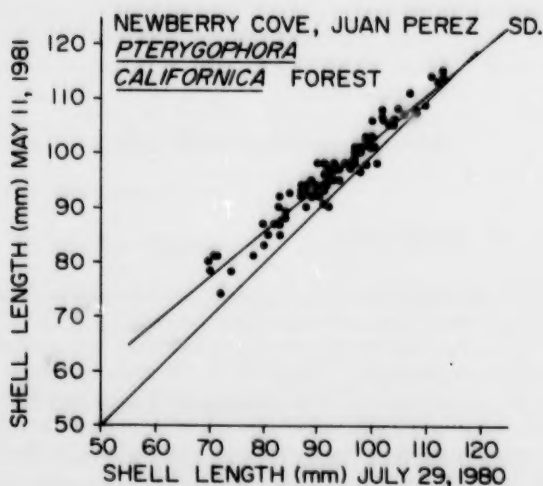
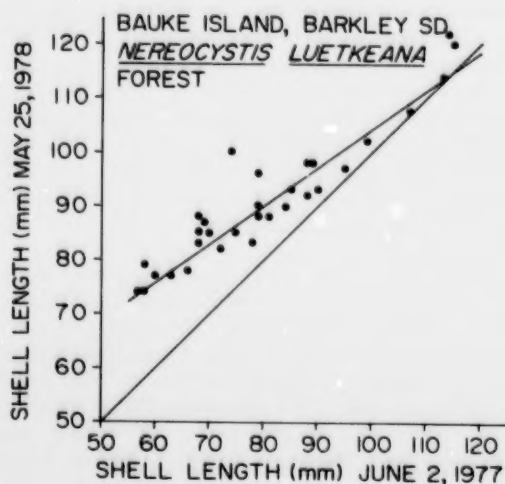
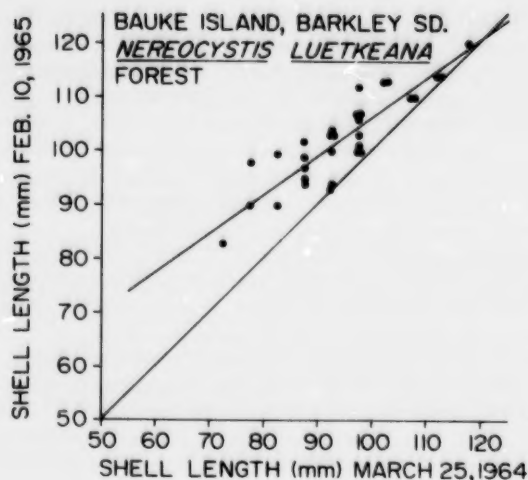


FIG. 5. Ford-Walford plots of growth of tagged *Haliotis kamtschatkana* at a Bauke Island, Barkley Sound, Vancouver Island *Nereocystis luetkeana* forest in 1964-65 (data from Quayle 1971) (top); at a Bauke Island *N. luetkeana* forest in 1977-78 (middle); at a Newberry Cove, Juan Perez Sound, Queen Charlotte Islands *Pterygophora californica* forest in 1980-81 (bottom) (from data in Breen and Adkins 1982).

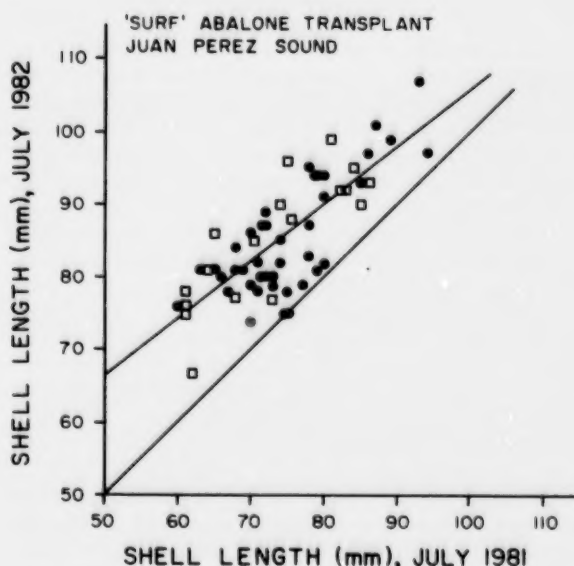


FIG. 6. Ford-Walford plot of growth of tagged *Haliotis kamtschatkana* transplanted from a *Pterygophora californica* forest at Hoskins Islet to a *Macrocyctis integrifolia* forest at Murchison Island, both in Juan Perez Sound, Queen Charlotte Islands. Dots are for abalone with legible tags; squares are for those with illegible tags whose initial lengths were estimated from the shell colour change resulting from change in diet after transplantation (from data in Breen and Adkins 1982).

differences between males and females at six different sites. However, there were different shell length and total weight characteristics among sites. The predicted weight of a legal-sized northern abalone (100 mm shell length) calculated from length-weight regressions of samples at different sites varied from 116.7 to 164.5 g (Breen and Adkins 1982). The regression of total weight and shell length from Ramsay Island, Juan Perez Sound is shown in Fig. 7. They suggested that abalone with slow growth rates, such as those in *Pterygophora* forests, were heavier per unit length as their shell volume was larger and shell height greater. Such high-spired shells have a thick growing edge and are often heavily encrusted with coral-line red algae.

Schnute and Fournier (1980) estimated growth parameters from northern abalone length frequency data with a non-linear estimation technique. They analyzed data from abalone collected in *Nereocystis* forests in the Queen Charlotte Islands (Breen and Adkins 1979). They estimated $L_{\infty} = 132.8$ mm and $K = 0.216$.

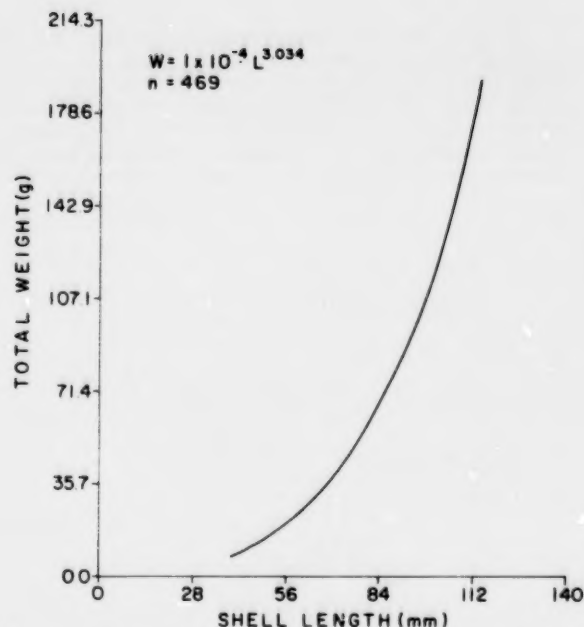


FIG. 7. Shell length-total weight relationship fitted by linear regression for *Haliotis kamtschatkana* from Ramsay Island, Juan Perez Sound, Queen Charlotte Islands (from Breen and Adkins 1982).

Quayle (1971) attributed similar growth increments in northern abalone populations separated by 563 km to similar temperature regimes. It seems more likely, however, that in British Columbia abalone growth rate is dependent on food supply (Breen 1980a, b) and exposure to high wave energy, i.e. "surf abalone" (Breen and Adkins 1979). Reasons for the smaller size of *H. kamtschatkana* in California (rarely > 100 mm shell length; Cox 1962) are unknown.

In a laboratory study on Alaskan northern abalone, Paul et al. (1977) reported that captive adults fed *ad libitum* showed negligible growth between mid-May to mid-August during gonad ripening and spawning. Moreover, sexually immature individuals grew more rapidly than mature adults. In other laboratory studies Paul and Paul (1981) found that growth was inhibited at 5.5°C and maximum at 13.5°C in northern abalone kept under non food-limited conditions. Breen (unpublished observations) collected 50 British Columbia northern abalone from 10 to 40 mm shell length and held them in the laboratory for several months at ambient temperature with *Nereocystis* food provided *ad libitum*. Growth varied with temperature as follows:

$$i = 0.0067 T - 0.0055$$

where i is the daily growth increment (mm) for a 30 mm long juvenile and T is temperature (°C). This agrees well with the growth curve in Fig. 4 of Paul et al. (1977).

Growth in northern abalone may be highly seasonal. In the Sitka Sound area (≈57°N), Paul and Paul (1981) reported that growth in field populations of northern abalone began at 13.5°C and in July and August, when temperatures were between 13 to 14°C, growth was fastest. Larsen and Blankenbeckler (1980) reported 130 tag returns (total of 1107 tagged at two sites) from

northern abalone at large from May to January (8 months) in southeast Alaska (≈55°30'N). Estimated annual growth increments were: < 50 mm shell length abalone grew 19.1 mm, 50 to 74 mm abalone grew ≈ 12.6 mm, 75 to 99 mm abalone grew ≈ 6.2 mm and > 100 mm abalone grew ≈ 4.3 mm. The onset of sexual maturity was suggested to be responsible for slowing the growth of larger abalone. They also suggested that growth slowed seasonally, during winter and spring.

Most authors have used the von Bertalanffy model for growth studies in *Haliotis* species, but Clavier and Richard (1985) fitted a Gompertz model. Tagging and recapture is a common method for the study of growth (e.g. Forster 1967; Newman 1968). Harrison and Grant (1971) suggest that some tags may impair growth. Sainsbury (1980) demonstrated the importance of considering individual variation in growth rate when estimating average growth rates in abalone, and presented a method for analysing increment data from tagging. Table 3 lists von Bertalanffy growth estimates for several haliotids.

Wright (1975) marked *H. cracherodii* by filing a mark into the shell apex. In some large abalones, length decreased because shell erosion was greater than growth over the period of study.

Modal analysis of length frequencies has been used, especially for estimating growth of juveniles: e.g. Newman (1968), Poore (1972a), Sainsbury (1982a), Clavier and Richard (1985; 1986a). Growth has been estimated from annual rings by Sakai (1960, 1962) and Kojima et al. (1977), who demonstrated Lee's phenomenon (Ricker 1975) in the back-calculated lengths.

It is well known that abalone growth varies within (Kojima et al. 1977; Mottet 1978), as well as between species. Sainsbury (1982a) reviewed intraspecific variations in haliotids growth according to locality and season. Locality is important to growth because of food supply (Breen 1980 a, b; Shepherd and Hearn 1983), exposure to wave energy (Breen and Adkins 1979) and local thermal conditions (Newman 1969; Leighton 1974). Season is widely reported to influence abalone growth through changing temperature and algal community conditions. Moreover, growth can be retarded by the diversion of energy into seasonal gonad production (Leighton and Boolootian 1963; Mottet 1978; Shepherd and Hearn 1983; Kim and Chung 1985; Clavier and Richard 1986a). Growth can also vary considerably between different conspecifics kept under the same laboratory conditions (Leighton 1972). In summary, the growth of abalone shows considerable variability in time and space.

4.44 Metabolism

The processes by which food is incorporated into abalone tissue and subsequently converted for special functions such as reproduction have not been well studied for abalone generally (Mottet 1978). Abalone are generally slow moving and slow growing molluscs. Metabolic rates are strongly influenced by temperature as indicated by manipulated growth rates in mariculture studies (McCormick and Hahn 1983; Uki 1984).

The feeding and growth rate of northern abalone in the laboratory depends upon temperature, body size and the type of food available (Paul et al. 1977; Paul and Paul 1981). Growth was best at 13° to 14°C in the range between 5 and 14°C. No specific information on the metabolic processes in this species is available.

4.45 Size and Age

Quayle (1971) proposed that British Columbia northern abalone take ≈ 7.4 yr to reach 100 mm shell length. Breen (1986) suggested that a minimum of 6 years is needed to recruit to the fishery after settlement. Age determination, however, is not possible (section 4.31). Growth varies markedly between different sites, which Fournier and Breen (1983) suggest could be associated with habitat-related mortality, growth rates and final size. Figure 8 illustrates differing growth curves of northern abalone sampled from three kelp forest types in northern British Columbia. "Surf" abalone, at particularly exposed sites such as *Pterygophora californica* forests, may never reach legal size. Larson and Blankenbeckler (1980) suggested that southeast Alaskan individuals reached 95–100 mm in seven growth seasons.

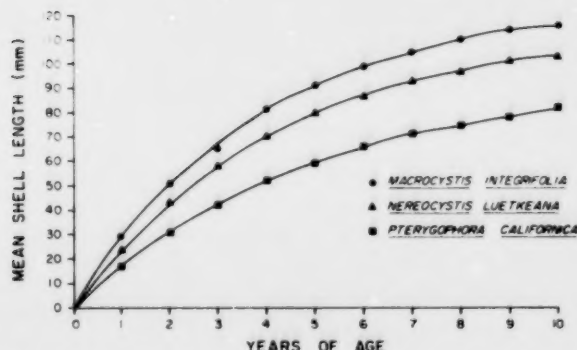


FIG. 8. Growth curves of *Haliotis kamtschatkana* collected in three different kelp forest types. The *Macrocyctis integrifolia* forest was at Murchison Island and the *Pterygophora californica* forest at Newberry Cove, both in Juan Perez Sound, Queen Charlotte Islands; the *Nereocystis luetkeana* forest was at Hickey Island, Estevan group of islands (from data in Breen 1980b). Purported "age" from shell characteristics.

5. Population (stock)

5.1 Structure

5.11 Sex Ratio

Northern abalone throughout British Columbia have a sex ratio of close to 1:1 (Breen and Adkins 1982; section 4.11).

5.12 Age Composition

The age composition of northern abalone populations is unknown as the species cannot be aged (section 4.31).

5.13 Size Composition

Size compositions of northern abalone populations have been used to estimate recruitment, growth and mortality in British Columbia (Breen 1986). Shell length frequencies of northern abalone were recorded by Quayle (1971) and the 14 British Columbia surveys (section 6.36).

All surveys measured length as shown in Fig. 4. Before 1978, samples for determining length frequencies were collected by haphazard swimming. This can bias the length frequency for three reasons. Smaller abalones are less visible than larger abalones, they tend to be cryptic, and they occupy deeper habitat than larger abalones. Length frequency samples collected in 1978 were collected as part of abundance surveys, and the first cause of bias was eliminated because divers searched thoroughly within quadrats. The survey protocol was changed in 1979 (Breen and Adkins 1981) to turn over all rocks (section 6.36), eliminating the second cause of bias. This leads to increased density estimates and greater numbers of smaller abalones are found (Boutillier et al. 1984). Stratified sampling, conducted to obtain length frequencies representative of the whole intensively sampled population in an area, was conducted in 1979 and 1980 (section 6.36).

A relative scarcity of small individuals was noted by Quayle (1971). Some of the apparent skewness in early size compositions results from the sampling biases discussed above. When intensive stratified quadrat sampling was conducted (Breen and Adkins 1982), small abalones were found at some sites in the relative abundances expected from equilibrium populations (Hoskins Islet in Fig. 9). At other sites, juveniles were scarce or absent (Lyell and Huxley Islands in Fig. 9).

Size compositions of northern abalone from different ecological communities vary (Fig. 10; Table 4). Few small abalones were found in *Macrocyctis* forests, where the largest adults occurred. At the other extreme, few large abalones were found in *Pterygophora* forests, where many juveniles were seen. Breen and Adkins (1979) suggested that the quantity and quality of food determines the growth rate at a site; while other factors unrelated to food or related to the habitat type determine settlement rate of juveniles.

Because the same sampling method was used at the three sites shown in Fig. 9, the apparent differences among sites must reflect real differences in juvenile abundance. Some northern abalone populations sampled in 1980 were not in equilibrium, and recent settlement of larvae was less than that required to maintain the existing population structure. This conclusion is supported by estimates of recruitment to the fishery and by results from stock reduction analysis, both of which are discussed below.

Populations with few small and many large individuals are common in *Haliotis* species (Hayashi 1980b; Sainsbury 1982a; Clavier and Richard 1985; 1986b). Hayashi (1980b), Sainsbury (1982a) and Shepherd et al. (1985) concluded that the patterns they observed resulted from unstable settlement patterns. Prince et al. (1987) suggest that dispersal of abalone larvae is extremely limited, and go on to suggest that settlement rate of juveniles relates

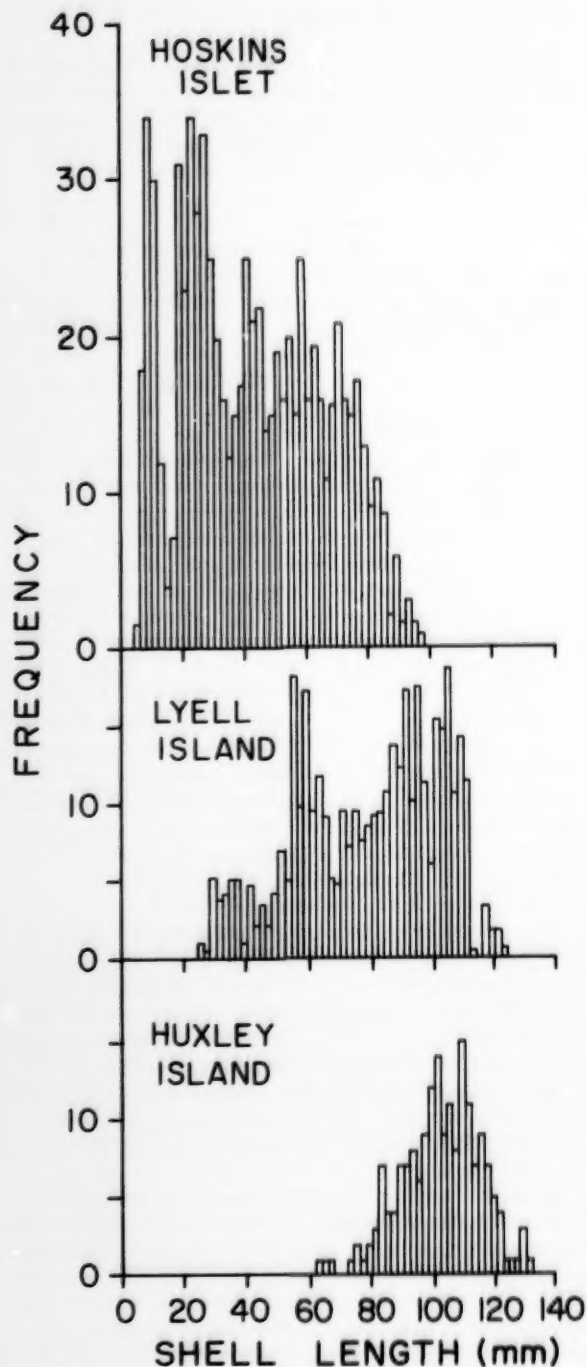


FIG. 9. Shell length frequencies of *Haliotis kamtschatkana* collected by stratified sampling at three sites in the Queen Charlotte Islands (from Breen 1986).

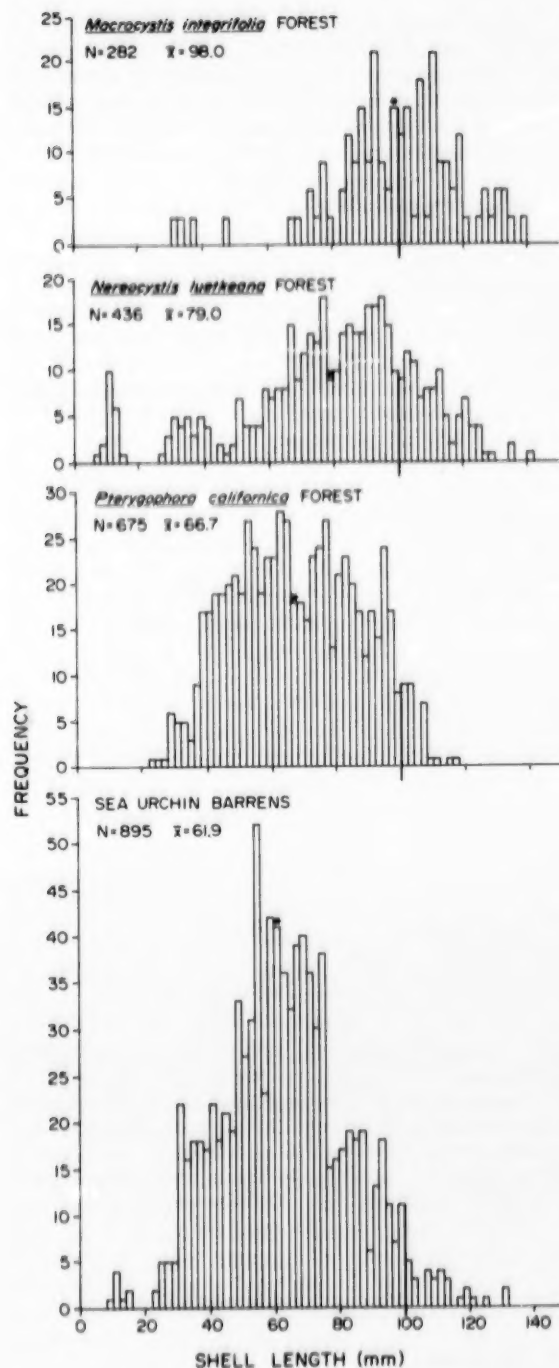


FIG. 10. Shell length frequencies of *Haliotis kamtschatkana* collected in 1978 according to three different kelp forest and sea urchin barrens habitats in the Queen Charlotte Islands (from data in Breen 1980b). Asterisks denotes sample means.

TABLE 4. *Haliotis kamtschatkana* size and density according to community characteristics in 93 sites from the east coast of Moresby Island, Fishery Statistical Area 2E (from Breen and Adkins 1979; Breen 1980b).

Community type ^a	Sites ^b	Habitat characteristics		Qualitative kelp characteristics		Mean Density (N·m ⁻²)			$\bar{x}$ max. length (mm)
		Relative exposure	Substrate	Growth form	Biomass	Total	Legal	Legal %	
bottom-form <i>Macrocystis</i>	0	very sheltered	loose substrate	dense bottom cover only	high	—	—	—	—
surface-form <i>Macrocystis</i>	20	sheltered/moderate	loose rock	canopy of floating kelp	high	1.1	0.52	46	128
<i>Nereocystis</i> / <i>Laminaria</i>	8	moderate	variable rocky	<i>N.</i> canopy/ <i>L.</i> understory	moderate	1.8	0.43	24	111
<i>Nereocystis</i> / annuals	11	moderate	variable rocky	<i>N.</i> canopy/ annuals understory	moderate	2.3	0.36	16	NA ^c
<i>Nereocystis</i> / <i>Pterygophora</i>	16	moderate	variable rocky	<i>N.</i> canopy/ <i>P.</i> understory	moderate	2.3	0.65	29	NA
<i>Laminaria</i>	4	moderate	variable rocky	understory, no canopy	moderate	3.8	0.76	20	NA
<i>Pterygophora</i> (no overcanopy)	7	moderate/high	smooth bedrock	dense understory	low	9.5	0.32	3	100
no kelps/sea urchins	27	highly variable	variable rocky	no kelp	virtually none	2.3	0.08	3	102

^a *Macrocystis integrifolia*, *Nereocystis luetkeana*, various *Laminaria* spp., *Pterygophora californica*.

^b Sites with countable abalone only, 6 bottom-form *Macrocystis* sites were surveyed — none had abalone.

^c A non-canopy growth form which lies prone over the substrate.

^d NA = Not available.

to density of spawners in the immediate vicinity. Sluczanowski (1984, 1986) has suggested a link between egg production and subsequent recruitment to the fishery (section 6.35).

5.2 Abundance (Density)

5.2.1 Habitat-Related Variability and Total Abundance

Estimating total biomass of northern abalone in British Columbia is not practical with direct stock surveys because of the tendency of the species to clump (Breen 1980b), to vary in population characteristics according to local habitat, and the great length of the coastline. Methods based on catch per unit effort (CPUE) have serious problems when applied to abalone (section 5.22). The importance of local substrate, exposure and kelp community species and growth form to the number and size of abalone listed in Table 4 is summarized in Table 5. Dense populations of bottom-form *Macrocystis* on very sheltered, loose substrate yield no abalone, whereas canopy *Macrocystis* in slightly more exposed habitats with a more rocky substrate sustain a few very large abalone, exposed *Pterygophora* communities on bedrock sustain dense populations of small abalone, although very few reach legal size (sections 4.43, 4.45, and 5.13). The most productive habitats for legal abalone have rocky substrates, moderate exposure and moderate algal productivity from both canopy- and understory-forming species (Table 6).

TABLE 5. Habitat and population characteristics of *Haliotis kamtschatkana* in two kelp forest types in British Columbia.

Northern abalone habitat and population characteristics	Kelp forest type	
	<i>Macrocystis integrifolia</i>	<i>Pterygophora californica</i>
Aspect	sheltered	exposed
Food	abundant	scarce
Food quality	high	low
Density	sparse	dense
Final size	large	small
Growth	fast	slow
Recruitment	low	high

Further complicating density estimation is the effect of depth. Breen and Adkins (1982) showed that density (and size) of abalone are greatest in the kelp zone, lower in the adjacent barrens immediately to seaward and lowest in the deepest, most seaward barrens (Table 6; section 3.2). This density pattern occurs irrespective of kelp community type and harvesting, with the exception of the Ramsay Island site.

Breen (1986) showed that between 1978 and 1984, total abalone abundance in the north coast of British Columbia decreased at survey sites (section 6.36) from 2.53–2.86 m⁻² to 0.65–1.91 m⁻². Virgin commercial

TABLE 6. Notes on *Haliotis kamtschatkana* abundance and recruitment of juveniles according to depth and habitat in six intensively sampled north coast British Columbia sites (from data in Breen and Adkins 1982).

Fishery Statistical Area	Locality	Previously harvested (Y/N)	Kelp type	Zone			Abalone			Notes on recruitment / sizes
				Type ¹	Width (m)	Sampled (m ²)	N	Density (N·m ⁻²) Total	Legals ²	
6	Weeteam Bay, Aristazabal Is.	Y	<i>Nereocystis</i>	1	2.7	57	324	5.7	0.47	low / numbers increase as size increases
				2	10.0	40	250	2.8	0.13	
				3	31.5	79	39	0.5	0.00	
6	Hickey Island, Estevan group	Y	<i>Nereocystis</i> / <i>Pterygophora</i>	1	50.0	20	63	3.2	0.55	very low / few small abalone recruited over the past few years
				2	125.0	20	52	2.6	0.10	
				3	125.0	40	43	1.1	0.03	
2E	Lyle Island	N	<i>Nereocystis</i>	1	7.0	50	240	4.8	1.42	low / numbers increase as size increases
				2	10.0	105	262	2.5	0.32	
				3	28.0	80	57	0.7	0.08	
2E	Hoskins Island, Juan Perez Sd	N	<i>Pterygophora</i>	1	8.5	51	654	12.8	0.02	high and regular / even decline in numbers as size increases
				2	10.0	50	413	8.3	0.00	
				3	19.0	27	48	1.8	0.00	
2E	Ramsay Island, Juan Perez Sd	Y	<i>Nereocystis</i>	1	6.6	46	239	5.2	0.35	high / decline in numbers as size increases
				2	10.0	35	181	5.2	0.00	
				3	5.0	25	198	7.9	0.00	
2E	Huxley Island, Juan Perez Sd	Y	<i>Macrocystis</i>	1 ³	8.7	173	192	1.1	0.55	very low / none <60 mm length

¹ Zone type 1 = kelp zone; 2 = barren zone 10 m wide, immediately seaward of kelp; 3 = lower barrens seaward of Zone 2.

² This locality had kelp zone only, with no barrens. The rocky substrate was replaced by sand at a shallow depth.

³ ≥ 101.6 mm shell length.

beds were estimated to have had a mean of ≈ 2.5 legal northern abalone m^{-2} (Breen 1980b; Bernard 1982). In 1983-84, north coast sites produced estimated mean densities from 0.10 to 0.31 legal abalone m^{-2} (Breen 1986). An estimate of total biomass of the stock when the intense fishery began in 1976 is available from stock reduction analysis (section 6.35). Breen (1986) estimated that the stock in areas available for harvest in 1976 was ≈ 1800 t at the beginning of 1976 and ≈ 450 t by the end of 1980.

5.22 CPUE as an Index of Abundance

Licence holders in British Columbia are required to furnish logbooks with basic catch and effort records (section 6.34). Values of CPUE, expressed as kg per diver day, are given in section 6.3. Breen (1980b) examined the relevance of CPUE data as a reflector of abundance in this fishery and concluded that CPUE was probably not useful.

Breen (1980b) and Fedorenko and Sprout (1982) reviewed problems with using CPUE in abalone stock assessment:

- 1) catches may remain high despite stock reduction because an increasingly large area will be accessed, increasing the ratio of search time to catch handling time (Beinssen 1979)
- 2) in a new fishery harvesters sequentially harvest virgin beds, thus maintaining a high catch rate while the stock as a whole decreases
- 3) the quality of effort varies greatly between divers and a diver's effort becomes more effective and CPUE increases (irrespective of stock size) according to a diver's personal learning experience

- 4) fishermen's logs often contain unreliable effort data; the number of hours dived would be much preferable to days dived
- 5) operations procedures vary considerably between vessels and their effort may not always be comparable
- 6) season changes can influence CPUE irrespective of stock size; a shortened season can intensify effort and maintain CPUE despite decreasing stocks
- 7) quotas tend to decrease effort intensity, particularly in a limited licence fishery where the quota is evenly shared, thus guaranteeing fishermen access to a known amount of catch
- 8) changes in Area openings and closures can influence effort, for example opening areas susceptible to harsh weather conditions or naturally less productive beds will cause increased effort irrespective of overall stock status

In a new fishery, divers gain experience, become more efficient over time, and change their behaviour in response to management actions (Harrison 1983). This effect tends to mask declining abundance. A similar argument was made by Newman (1967).

When CPUE (section 6.3) in the British Columbia northern abalone fishery is compared with other estimates of abundance, these arguments are supported. CPUE from 1976 to 1980 decreased by 36.6%, while the total biomass estimated from stock reduction analysis (section 6.35), declined by 75.0%. CPUE does not appear to be useful as a direct index of relative abundance in this fishery. It might still be useful, as Fedorenko and Sprout (1982) suggest, to consider declining CPUE as an indicator of declining stock size.

5.23 Density as an Index of Abundance

No density estimates of northern abalone were made in British Columbia before 1976. A rough estimate of mean density in unfished beds was obtained from discussions with fishermen of that period and with biologists who had worked on abalone before 1976. This estimate was 2.5 m^{-2} (Breen 1980b; section 5.21).

In 1976 density estimates were made during surveys (section 6.36). A standard density survey technique was adopted in 1978 and has been used with minor modification since then. Although the procedure has been standard, estimates have not been made in any systematic way in any area. These estimates are given below (section 6.36) and will only be summarized here.

In an extensive survey of the eastern Queen Charlotte Islands (Breen and Adkins 1979), mean density was $> 16 \text{ m}^{-2}$ and ranged from 0 to 28 m^{-2} ; the highest density observed within one 1 m^2 quadrat was 56. Some of the variation in abundance could be explained by habitat type (Tables 4 and 6). However, this relation was quite different from the relation between growth and habitat. Abalone were most numerous in *Pterygophora* forests, where food is limited and probably of poor quality. They were not numerous in *Macrocystis* forests, where the preferred food is abundant. It is therefore necessary, when considering abundance of *H. kamtschatica*, to maintain an ecological context and to consider the sampling design in relation to community structure and depth. Changes in abundance will be discussed in connection with the fishery in section 6.4.

5.3 Recruitment

Recruitment is defined here in the fisheries sense as the rate at which abalone become vulnerable to the fishery. The overfishing of abalone appears to be widespread (Harrison 1986), with their apparent susceptibility to

"recruitment overfishing" (Gulland 1973, 1983) in which spawning stock is reduced to such a level that inadequate production of recruits ensues. Prince et al. (1987) believe that the density of abalone settlement is related to "immediate density of spawning abalone" due to extremely limited larval dispersal, i.e. a clear stock-settlement relationship. They believe that patterns of recruitment related to differential patterns of mortality after settlement.

Breen (1986) estimated recruitment in northern abalone from size frequencies and growth data. Northern abalone recruitment, as with other aspects of their life history, varies according to habitat as shown in Table 6. Because settlement takes place deeper than the adult population (section 3.2), this may involve both growth and migration. Growth is probably the more important process. From survey data one can estimate the densities of pre-recruits and new recruits, defined as those individuals which will grow or have grown, respectively, to legal size within one year. This has been done using field survey data from several years (Table 7). The values seen in Table 7 are less than those required to maintain an equilibrium population at the pre-fishery density. If the natural mortality rate (M) is 0.20 (section 5.4) and the pre-fishery density was 2.5 m^{-2} (section 5.23), then the densities of pre-recruits and new recruits required (Breen 1986) would be 0.55 and 0.45 m^{-2} respectively. The observation that present recruitment is well below these values suggests that settlement has not been stable in this fishery.

Causes of poor recruitment in northern abalone are not well understood (Breen 1986). The fishery could have influenced recent recruitment, but there appears to have been a recruitment failure prior to the period of intense harvesting begun in 1976, and another in the 1950's (Quayle in Breen 1986). In the Channel Islands low settlement of *H. tuberculata* in an excessively cold winter contributed to the overall population decline influenced by harvesters (Forster et al. 1982). Altered current

TABLE 7. Numbers of "pre-recruit" and "new recruit" *Haliotis kamtschatica* observed during quadrat sampling along the British Columbia coast in the years shown. "Pre-recruits" were defined, based on growth estimates, as individuals with lengths of 94.0-101.5 mm; "new recruits" as those with lengths 101.6-107.0 mm. Replacement densities were estimated as described in Breen (1986), assuming a mean unharvested density of 2.5 legal-sized individuals/ m^2 and $M = 0.20$. From Breen (1986), Boutilier et al. (1985), Farlinger and Bates (1986), and Carolsfeld et al. (1988).

Year	# sites	# m^2	Pre-recruits	#/ m^2	New recruits	#/ m^2
1978	45	746	198	0.265	175	0.235
1979	33	1416	489	0.345	357	0.252
1983	32	512	118	0.230	56	0.109
1984	70	1120	68	0.061	32	0.029
1985	11	176	35	0.199	28	0.159
1987	63	1008	56	0.056	52	0.052
Total	254	4978	964	0.194	700	0.141
Replacement densities				0.554		0.453

patterns during an El Niño were speculated to have reduced recruitment of red abalone *H. rufescens* off southern California (Tegner and Dayton 1987). Using shell length frequency data from an unharvested population of *H. iris* in New Zealand, Sainsbury (1982b) constructed a population model. The observed abalone sizes, representing a non-stable accumulation of older individuals, were best described by an ≈ 5 yr period of high recruitment preceded and followed by longer periods of low recruitment. In a 17-yr study of an unfished *H. laevis* population, wide interannual variations in recruitment of two-year-olds occurred (S. A. Shepherd, South Australia Department of Fisheries, pers. comm.). Successive years of strong recruitment led to marked population increases, followed by density-dependent mortality, only twice during the study. Breen (1986) reviewed the literature and concluded that significant natural fluctuations are a molluscan characteristic and that physical environmental variables can intercede to prevent full settlement success in abalone.

Estimates of settlement in *Haliotis* were rarely published before Sainsbury's (1982a) work. Small abalone are highly cryptic (section 3.21) and thus have a history of being overlooked in field surveys. Speculations about abalone settlement range from high for *H. rufescens* in central and southern California, where populations persist despite high predation pressure (Hines and Pearse 1982; Tegner and Butler 1985b), to low and unstable due to climate effects influencing poor spawning years (Hayashi 1980b; Sainsbury 1982a; Shepherd et al. 1985).

5.4 Mortality

Haliotids are generally considered to have low instantaneous rates of natural mortality (M) (Shepherd et al. 1982). In unharvested populations, M usually ranges between 0.1 and 0.2 (Sainsbury 1982a; Shepherd et al. 1982; Harrison 1986) and these populations are characterized by accumulations of larger, older individuals (Hayashi 1980b; Sainsbury 1982a; Breen 1986; Clavier and Richard 1985, 1986b). A low value of M is reasonable considering the relatively long life and slow growth of abalone (Beinssen and Powell 1979).

Little is known about the causes of mortality in *H. kamtschatica*. Some known predators of adults are discussed in section 4.34, but predators of juveniles are unknown. Juveniles are likely to have higher mortality rates than adults. In larger abalone, mortality may be size-independent (Sainsbury 1982a), although in some areas specialized predators such as sea otters target on larger abalone (Hines and Pearse 1982).

Thermal mortality of northern abalone occurs in the laboratory at constant temperatures $> 16^\circ\text{C}$ (Paul and Paul 1981). In culture, Beaudry (1983) found that larval northern abalone survived best from fertilized egg to trochophore at 14°C , reached greatest size at settlement when reared at 18.5°C , but grew most rapidly and achieved greatest post-settlement length within two months at 16°C . There was total larval mortality at 21°C . Abalone generally prefer full salinity seawater and we suggest that temperature and salinity conditions may limit distributions (section 3.22). In nature episodic high temperatures or low salinities may have caused mass

mortalities. Storms can cause mortality and Thompson (1914) described northern abalone washed ashore after winter storms.

Starvation is reported in Japanese abalone as a consequence of decreased brown algal production (Tanaka et al. 1986c). Kelp forests are sensitive to environmental events (Dayton and Tegner 1984; Zimmerman and Robertson 1985) such as El Niños and storms which may be an indirect cause of abalone mortality. Parasites are implicated in declines in *H. laevis* in nature (section 4.35).

An obvious and important source of mortality is fishing. The instantaneous rate of fishing mortality is F [$F + M = Z$ the total instantaneous rate of mortality Ricker (1975)]. Less obvious is mortality caused by fishing which does not contribute to the catch. A diver, uncertain whether an abalone is of legal size, may remove it from the rock for measuring. Even if measured underwater and replaced immediately, its chance for survival is decreased. Until the animal is firmly re-attached, it is vulnerable to injury or predation (McShane and Smith 1986). If the foot has been damaged during removal, the abalone is especially vulnerable. This is a significant cause of mortality in the fishery for *H. rufescens* (Burge et al. 1975; Tegner et al. 1988). In the fishery for *H. kamtschatica*, abalone are sometimes measured aboard the tender boat and simply thrown back into the water. One of us has observed abalone returned in this way landing on sand. The overall mortality caused by improper handling of sub-legals might be significant.

Because northern abalone cannot be aged, natural mortality rate must be estimated either through tagging or by analysis of length frequency distributions. The rate of tag recaptures after one year in growth studies is about 5% (Table 1), but survival is unlikely to be this low. Tag recapture rates can be reduced by migration, tag loss, mortality caused by handling, and perhaps by differential predation on tagged animals.

Emmett et al. (1988) wired stainless steel discs to the shells of northern abalone, and collected all tagged empty shells in regular visits to their transplant and control sites (sections 4.43, 6.5). Recapture rates were 39–73%, and with the recovery of empty tagged shells, 55–88% of the tagged abalones were accounted for. Recovery of live animals gives a minimum estimate of survival and maximum estimate of mortality; the latter ranged from $M = 0.48$ to 2.51 at four sites. Recovery of dead shells gives a maximum estimate of survival and minimum estimate of mortality: $M = 0.15$ to 0.27. Table 8 lists some estimates of M , and their methods of calculation, from other *Haliotis* species.

Breen (1980b) used Heincke's (Ricker 1975) and Van Sickle's (1977) methods to obtain estimates of $Z = 0.13$ to 0.54 from various length frequency samples in *H. kamtschatica*. Fournier and Breen (1983) and Breen and Fournier (1984) describe a method for estimating mortality rates from size frequency distributions. A non-linear technique simultaneously estimates mean lengths-at-age, standard deviations of lengths-at-age around their mean, cohort abundances, variances of the means around a von Bertalanffy curve, and cohort abundances around a smooth exponential decay curve.

TABLE 8. Estimated instantaneous rate of natural mortality (M), and method of estimation for various *Haliotis* species.

Author	Species	M	Data source and/or method of mortality estimation
Beinssen and Powell (1979)	<i>H. rubra</i>	0.20	Repeated tag-recapturing
Shepherd et al. (1982)	<i>H. rubra</i>	0.21-0.36	Tag-recapture
	<i>H. laevigata</i>	0.22-0.26	Tag-recapture
Shepherd (1986b)	<i>H. laevigata</i>	0.59	Tag-recapture (different site than Shepherd et al. 1982)
Sainsbury (1982a)	<i>H. iris</i>	0.10	Beverton and Holt (1956) and Ssentongo and Larkin (1973) based on shell length and growth rate data; developed own model
Olsen (1971) (in Sainsbury 1982a)	<i>H. fulgens</i>	0.07	Ursin (1967)
Tutschulte (1976)	<i>H. fulgens</i>	0.90 (ages 1 to 6)	3 methods: survival rates calculated over 4 month intervals from dead shell collections; polymodal analysis of shell length frequencies and constructed life tables using the estimated age compositions; compared age distributions in two consecutive years
	<i>H. corrugata</i>	0.20 (> 7)	
		0.70 (ages 1 to 7)	
Doi et al. (1977)	<i>H. corrugata</i>	0.35-0.43	Population model and CPUE data
Clavier and Richard (1985)	<i>H. tuberculata</i>	0.14-0.20	Tag-recapture and population modeling
Tegner et al. (1988)	<i>H. rufescens</i>	0.10-0.15	Fournier and Breen (1983)

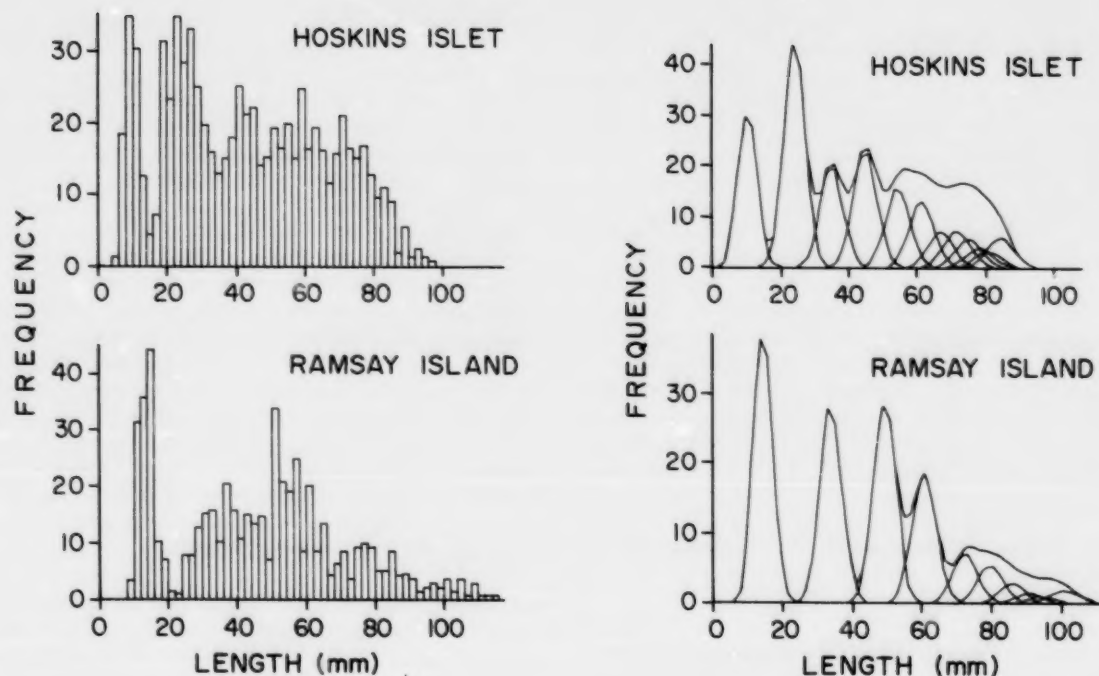


FIG. 11. Shell length frequencies of *Haliotis kamtschatkana* collected by stratified sampling from two Juan Perez Sound, Queen Charlotte Islands sites, and the corresponding results of the mortality estimation procedure (from Fournier and Breen 1983). Each curve in the right side graphs is a single age class. The uppermost curve in each right side graph is the sum of all age classes.

TABLE 9. Mean lengths of *Haliotis kamtschatkana* from north coast commercial fishery port sampling in Prince Rupert, B.C. 1982 to 1985 (from Farlinger and Bates 1986).

Statistical Area	Year	n	$\bar{x}$ Shell length (mm)	Legal-sized (%)
1	1984	187	111.1	97.9
	1985	65	112.5	100
5	1984	40	114.3	100
6	1982	662	115.7	NG*
	1983	262	108.2	96.9
	1984	349	109.9	98.6

* NG — not given.

The application of this method to stratified sampling data from Hoskins Islet and Ramsay Island, Juan Perez Sound, is shown in Fig. 11. The method was used on 15 sets of data where the whole population was sampled (Breen 1986). Total instantaneous mortality rate estimates ranged from $Z = 0.05$ to 0.41 , and were highest at sites exposed to the commercial fishery. Estimates from sites within closed areas should indicate instantaneous natural mortality rate: $M = 0.15$ to 0.20 . In laboratory grow-out of cultured *H. kamtschatkana*, Olsen (1984) obtained 70% survival ($M = 0.36$) over three years for individuals > 10 mm.

Fishing mortality rate is difficult to estimate. A small amount of northern abalone catch (port) sampling was conducted at Prince Rupert from 1982 to 1984. Table 9 shows that mean length in the catch is 112 mm. The minimum size is 100 mm, and 2-3 yr would be required for an abalone to grow 12 mm from legal size. This suggests that fishing mortality rate was moderate for the few years prior to catch sampling. The instantaneous fishing mortality rate (F) for northern abalone was estimated by stock reduction analysis (section 6.35). From this analysis, during the period 1976-80, F varied from 0.18 to 0.66.

Fishing mortality rate has not been estimated in many other abalone species. Beinssen (1979) estimated fishing mortality rate by placing tagged cans on a small reef and asking abalone (*H. rubra*) divers to collect and return them. He estimated $F = 0.80$ to 1.05 . Clavier (1982) used Beverton and Holt's (1956) method to obtain Z , then was able to subtract the simultaneously estimated M . Kojima et al. (1977) estimated $F = 1.8$ to 2.5 in *H. discus discus*, using daily catch records and DeLury's method (Ricker 1975). Smith (1972) used a method based on growth and length frequency data to estimate $Z = 0.05$ in an "old population" of *H. rufescens*.

6. Exploitation and Management

6.1 Introduction

Northern abalone are sought by three user groups in British Columbia. Native Indians were the first to exploit northern abalone and their fishery continues under regulations that recognize the special status of natives (section 6.21). The recreational fishery probably involves many more people, but little is known about this harvest (section 6.22). The commercial fishery, which likely accounts for

most of the total landed catch, has attracted the most management and research attention (section 6.3). Jurisdiction over northern abalone in British Columbia lies with the federal Department of Fisheries and Oceans, Pacific Region. The different user groups affect the northern abalone resource, and benefit from the resource, in different ways.

6.2 Non-Commercial Exploitation

6.21 Native Indian Fishery

Harvesting of *H. kamtschatkana* along the northwest coast of North America is an ancient native Indian activity. Although abalone shell was frequently used as an appliqué in northwest coast Indian art, northern abalone shell was infrequently used in comparison with *H. fulgens* and *H. rufescens* from California made available by trading (Holm 1965).

The right of native Indians to harvest northern abalone in British Columbia continues to be recognized. This fishery occurs mostly on the northern coast and almost exclusively involves hand picking from the intertidal zone. Upon request, a multispecies Indian Food Fish License is issued to native Indians which includes the right to harvest northern abalone. There is no limit on catch, but the minimum legal size of 100 mm shell length must be observed. The local Fishery Officer may attach to the License a request for provision of data on fishing locality and catch, but compliance is rare and virtually no enforcement is exercised. Few data on the native Indian abalone food fishing are available, and its relative extent is unknown. Virtually all areas are open to the Indian food fishery and some specific closures to the commercial fishery were established to ensure resource availability to natives (section 6.32). We believe this is the smallest of the three northern abalone fisheries in British Columbia.

6.22 Recreational Fishery

There has been a widespread recreational fishery for northern abalone in British Columbia waters, especially since the advent of SCUBA diving. The minimum legal size is 100 mm shell length and shells must be retained if the abalone are shucked to establish compliance with the legal size. Neither suction devices nor pointed instruments can be used to take abalone while diving or shore picking. There is a daily bag limit of 12 in Fishery Statistical Areas 1 to 10 (north coast), 6 in Areas 11 to

17 and 21 to 29, and 4 in Areas 18 to 20 (section 6.32).

In the Strait of Georgia, where northern abalone are not particularly abundant, recreational divers take only 1 172 abalone per 1000 dives (McElderry and Richards 1984). Recreational diving fisheries in British Columbia are difficult to sample because of their widespread nature, large number of participants and differing collection activities (Carmichael and Bourne 1986). Although divers undoubtedly take closer to their bag limits in better abalone areas such as the west coast of Vancouver Island and the north coast, their effect on stocks is considered minor (Breen 1986).

Washington State regulations permit a daily bag of 5 with a minimum legal size of 89 mm shell length. Recreational divers take $\approx 38\,600$ abalone annually from northern Puget Sound (91%) and the Juan de Fuca Strait/San Juan Islands (9%) areas (Bargmann 1984). From 6 to 18% of Washington State recreational divers report abalone catch, which is third in preference after Dungeness crab (*Cancer magister*) and scallop (*Crassidoma giganteus* and *Chlamys* spp.) (Bargmann 1984).

In southeast Alaska there is no recognised recreational fishery but rather a "subsistence" (food) fishery for native Indians and others. There is a daily bag limit of 50 and a minimum legal size of 95 mm shell length (termed maximum shell "diameter"). No total catch estimates for the subsistence fishery are available. Subsistence harvesters have access to all beds whereas commercial harvesters are excluded from certain beds set aside for the former (T. Koeneman, Alaska Dep. Fish and Game, pers. comm.).

6.3 Commercial Fisheries

6.3.1 History

The first record of the commercial fishery in British Columbia is provided by Thompson (1914), who makes reference to canning at some time previously in Bella Bella, Lizzie Cove (Jedway Bay) and Rose Harbour in the Queen Charlotte Islands, and drying at Murchison Island, Juan Perez Sound in the Queen Charlottes. Thompson stated that: "These operations have now been nearly entirely abandoned, mainly because of the difficulty that the Japanese have in obtaining a license, for they are the only people who appear to have interested themselves in the subject." Dalzell (1973) described these operations as taking place from 1910 to 1913 except for the Jedway Bay cannery, which continued for some time past 1926. The market seems to have been entirely "the Oriental market" (Thompson 1914). Thompson stated that both "diving" and "long poles armed with hooks" were used to catch abalone, but did not state what method of diving was used.

Very little is known about the commercial fishery between 1913 and 1952. Quayle (1962) stated: "Production has been erratic and at a low level, for as recently as 1958 only 100 cases were packed [5.3 t, Fedorenko and Sprout 1982] while 120 cases [6.4 t based on the conversion rate just shown] were produced as early as 1922". A record pack of 578 cases [30.6 t] was canned in 1928. Canneries were located at Jedway in the Queen Charlotte Islands, and at Bella Bella and Alert Bay.

SCUBA diving appeared in British Columbia in the 1950's, and commercial abalone harvesting was an obvious professional outlet for early divers. Annual landings for the first 20 yr documented (to 1971) are shown in Fig. 12. During this period production fluctuated considerably and only once (1964) did reported landings exceed those of the 1928 peak of 30 t. Fluctuations between years were large, and the sources of landings also varied greatly from year to year (Fedorenko and Sprout 1982). This pattern suggests that small enterprises developed in various areas at different times, and either went out of business quickly or shifted their attention to a different area. The market during this period was domestic, with abalone sold fresh to restaurants and fish stores. Prices during this period ranged from \$0.15 kg⁻¹ in 1954 to \$0.92 in 1970.

Landings, value, fishing effort and regulations for the British Columbia commercial abalone fishery from 1972 to 1986 are listed in Table 10. In 1972, the fishery increased to a new record production of 60 t. It remained near this level until 1976, when landings soared to 274 t before being stopped by an early closure. The new interest in abalone from 1972 onwards and the "gold-rush" (Breen 1986) of 1976 can be explained by a number of events. First, access to the salmon and roe herring fisheries had become restricted. Two effects were that holders of limited licenses amassed capital and in many cases invested in modern vessels. Some then looked for new fishing opportunities outside the salmon and herring seasons. Second, new entrants to fishing were forced into those fisheries with unrestricted access such as abalone. The fishery for geoduck clams (*Panope abrupta*), red sea urchins (*Strongylocentrotus franciscanus*) and prawns (*Pandalus platyceros*) all began or increased at this same time, for the same reasons. Third, a market for northern abalone developed in Japan. Accordingly, the price rose rapidly from \$0.99 kg⁻¹ in 1972 to \$3.14 kg⁻¹ in 1976. Fourth, technological changes allowed the fishery to evolve away from day-boat to freezer-boat enterprises. On-board freezers became common in the early 1970's. Light, portable diving

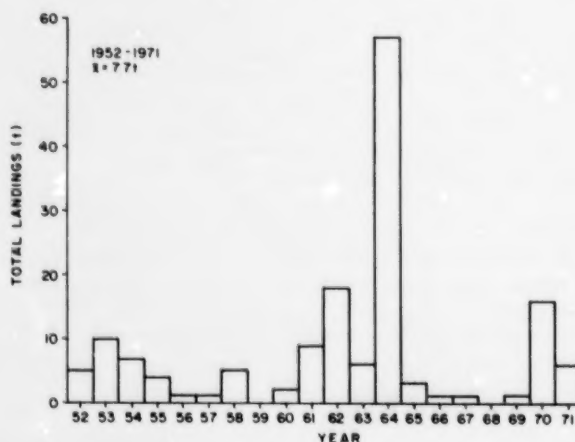


FIG. 12. Annual landings in whole, live weight (t) of *Haliotis kamtschatkana* in British Columbia between 1952 and 1971 (from Fedorenko and Sprout 1983).

TABLE 10. Northern abalone *H. kamischatkana* commercial fishery landings, value, effort, CPUE and regulations in British Columbia between 1972 to 1986. Data from Fisheries Branch, Dep. of Fisheries and Oceans, Fedorenko and Sprout (1982), Farlinger and Bates (1985), and Breen (1986).

Year	Landings (t)	Landed value (\$ × 10 ³)	Price (\$ t ⁻¹)	Effort			CPUE $\bar{x}$ kg/diver d	Regulations				
				No. of vessels	No. of divers	$\bar{x}$ no. of diver d/vessel		Licences		Quota (t)	Legal size shell length (mm)	Season (mo)
								No.	Type			
1972*	60	59	983	NA*	NA	NA	NA	open	C	none	90*	12
1973	68	94	1382	NA	NA	NA	NA	open	C	none	90*	12
1974	26	43	1654	NA	NA	NA	NA	open	C	none	90*	12
1975	59	132	2237	NA	NA	NA	NA	open	C	none	90*	12
1976	274	860	3139	NA	NA	NA	NA	open	C	none	90*	10.5
1977	428	1733	4049	22*	56	109	199	29*	C	none	101.6	8.0
1978	433	1864	4305	25	78	86	187	27	E	none	101.6	3.0
1979	186	1062	5710	25	59	54	155	26	E	226.8	101.6	7.5
1980	97	601	6196	25	33	32	131	26	E	113.4	101.6	7.5
1981	85	795	9353	24	33	29	134	26	E	94.3	100	7.5
1982	82†	457	8463	22	28	27	136	26	E	94.3	100	7.5
1983	56	464	8286	22	28	19	128	26	E	70.6	100	7.5
1984	58	530	9138	16	24	30	114	26	E	58.9	100	7.5
1985	44	442	10524	15	31	30	99	26	E	47.2	100	11.0
1986*	45	642	14287	18	29	25	115	26	E	47.2	100	11.0

^a Landings first recorded in 1952.

^b NA = not available.

^c Converted here to shell length from 2.5 inches shell width.

^d Reporting landings.

^e Licences are personal, not necessarily attached to a vessel and a licensee can hire other divers.

^f The first year in which landings from sales slips (54 t) were checked against log book returns (+ 28 t) for a total of 82 t.

^g Landings, value, catch and effort data for 1986 are preliminary.

compressors, combined with freezers, allowed vessels to become independent of shore facilities and exploit remote parts of the coast. The huge increase in landings in 1976 came from the north coast, only lightly harvested before 1973 (section 6.32). Finally, dry diving suits appeared in the late 1960's which allowed divers to spend as much as 8-10 h in the water in one day.

After 1976, landings were strongly influenced by management actions further described below. They increased to a peak of 433 t in 1978 (with a wholesale landed value of \$1.86 million), then declined under quota management to the present level of 47.2 t (Table 10). The wholesale price has continued to increase steadily (Table 10), and in 1987 exceeded \$18 kg⁻¹.

In 1981 the industry organized itself into the Abalone Harvesters Association to represent its interests in management of the resource. A committee of five licence holders and Fisheries personnel was formed to aid in reviewing licensing policy and biological management programs (Sprout 1983). By then the fishery was undergoing steady quota reduction and resource depletion was evident. The Abalone Harvesters Association remains intact and some of its members have joined the Underwater Harvesters Association which represents all diving fisheries. In 1987, as part of coordinating the overall shellfish advisory process, the Abalone Harvesters Association became a member of the Dive Fisheries Subcommittee reporting to the Shellfish Advisory Committee which aids management of invertebrate fisheries along Canada's Pacific coast.

6.32 Fishing Areas

In British Columbia, the nearshore coastal zone is divided into 29 Statistical Areas for fishery management purposes. The "north coast" consists of Areas 1 to 10

north of Cape Caution (Fig. 13), the "south coast" covers Areas 11 to 27 south of Cape Caution and the "Fraser River" comprises Areas 28 and 29 (Fig. 14), but does not contribute the abalone fishery. Between 1952 and 1960, landings from Area 12 on the south coast represented 94.5 % of total landings and north coast Area 5 represented 4.8 % (Fedorenko and Sprout 1982). The recent domination of landings from the north coast is shown in Fig. 15. The landings according to individual Statistical Areas from 1961 to 1986 are illustrated in Fig. 16. The major landings in the recent fishery have been from Statistical Areas: 1-north side of Queen Charlotte Islands; 2E-east side of Queen Charlotte Islands; 5-Banks Island area; 6-Caamano Sound/Estevan Group/Aristazabal Island.

Over the years there has been a complex patchwork of Area and sub Area closures as described by Fedorenko and Sprout (1982), Sprout (1983), Bates (1984, 1985) and Farlinger and Bates (1985). The reasons for these sometimes small, localized closures vary greatly. Common considerations are: exclusive recreational harvesting, exclusive native Indian harvesting and reduced stocks. Each Area is under the control of local Fishery Officers who have the final decision on closures. Often, management biologists are asked by Fishery Officers to provide technical advice on the advisability of a closure.

6.33 The Present Fishery

Most abalone boats now operating in the British Columbia fishery are multi-purpose inshore vessels < 25 m long. There have never been restrictions on vessel characteristics. Dive tenders are small vessels used to support the actual diving, and range from inflatables to 8 m aluminum herring skiffs. The fleet now comprises < 20

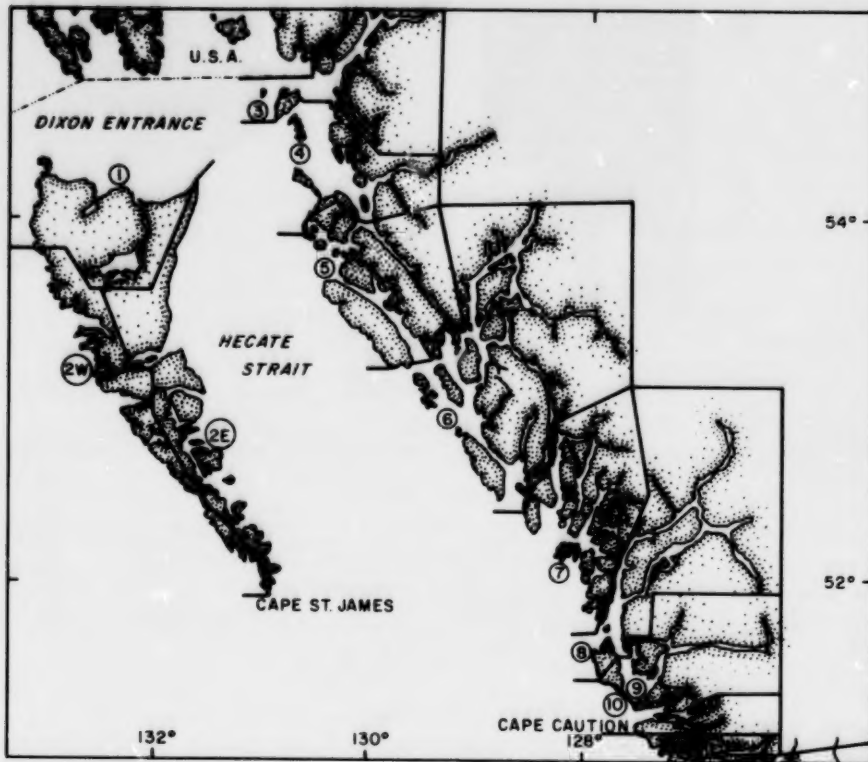


FIG. 13. Department of Fisheries and Oceans nearshore Fishery Statistical Areas (1 to 10) of the north coast of British Columbia.

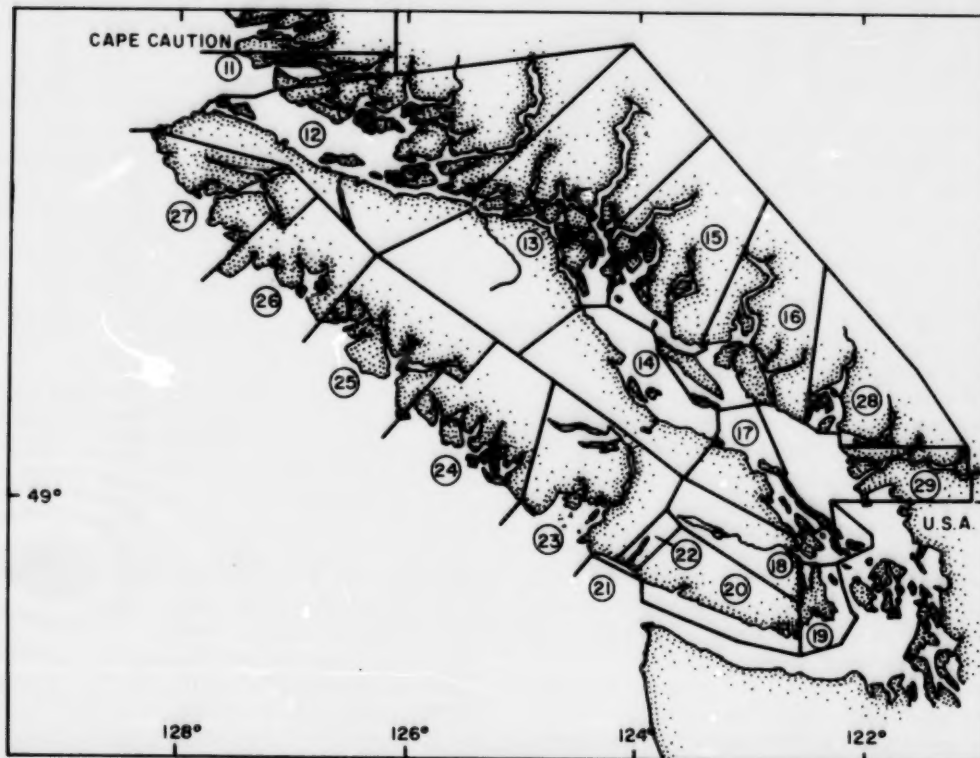


FIG. 14. Department of Fisheries and Oceans nearshore Fishery Statistical Areas (11 to 29) of the south coast of British Columbia.

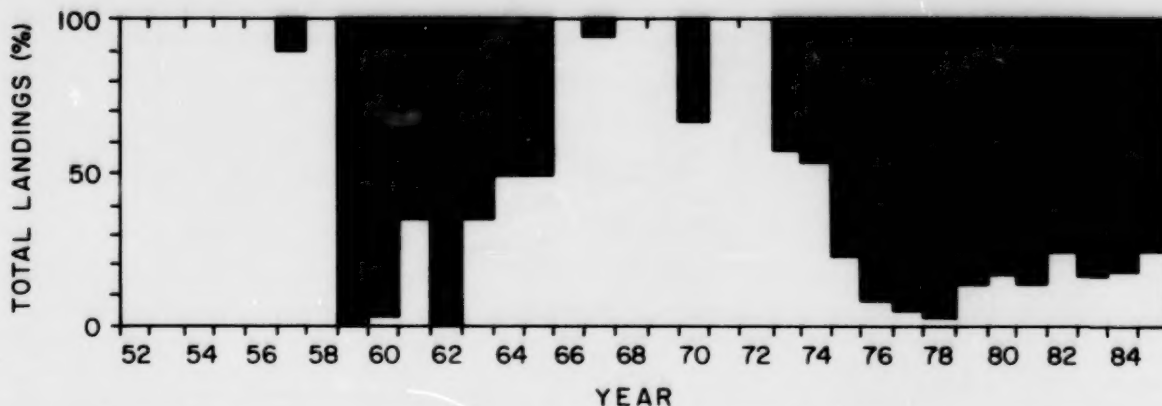


FIG. 15. Proportion of total annual *Haliotis kamtschatkana* landings from the north (black) and south (white) coasts of British Columbia between 1952 and 1985 (from Fedorenko and Sprout 1983, Farlinger and Bates 1985 and Fisheries Branch, Department of Fisheries and Oceans).

vessels, ≈ 30 divers and between 25 to 30 diver days per vessel are required to reach the quota (Table 10). Catch per unit effort (CPUE) has, after a period of steady decline since 1977, levelled off between 99 to 115 kg $\cdot$ diver day $^{-1}$.

Harvesters must notify the appropriate Fishery Officer before fishing in an Area, and prior to leaving the Area. Landed product must be weighed at unloading and the license validated by a Fishery Officer before the next trip. This is to ensure that the quota is not exceeded.

Divers use conventional SCUBA gear. They sometimes dive to 15 m, but normally work in shallow water and even harvest above chart datum. Pointed instruments or suction devices are not permitted as tools to remove abalone from the substrate. Blunt-ended bars are permitted.

Northern abalone are landed either frozen or fresh. Most are frozen whole, in the shell, and after initial freezing are "glazed" by dipping in seawater to prevent dehydration. If landed frozen, an allowance of 7% is made for the weight of the glaze which has been in effect since 1981 (Sprout 1983). Shells cannot be removed from abalone until after the catch is landed so that compliance with the size limit can be checked. Most product is exported to Japan, and a small amount is sold to domestic restaurants and through the retail trade.

Important sources of management information are log books and landings data. As a condition of their license, harvesters must provide their logs to the Fisheries Branch (management arm) of the Department of Fisheries and Oceans either monthly or shortly after the end of the fishing season. These confidential logs contain the number of diving hours and weight of catch taken by each diver on a vessel, date, Fishery Statistical Area or Sub-area and specific harvest location with sketch maps. Landings data are compiled by Fisheries Branch from sales slips provided by processors who have bought product from harvesters. Since 1982 sales slip data has been checked against harvester's log books to enhance the accuracy of landings data. Management biologists also receive anecdotal observations as to the well-being of populations of specific localities from harvesters.

Measuring of commercial catches has occurred in Prince Rupert since 1982 (Table 9).

A chronic problem of poaching exists in the British Columbia abalone fishery (Breen 1984; Sloan and Farlinger 1987; Jamieson 1988). This can be harvesting sublegal abalone, fishing in closed areas or exceeding quota. Individuals are enticed by the high value of abalone. Fishery Officers have difficulty in providing adequate surveillance over most of British Columbia's wilderness coast, and must expend most of their energies on large fisheries such as salmon and herring. An exception is the southern tip of Vancouver Island (Statistical Areas 19 and 20) where over 20 convictions have been made against abalone poachers (R. Kehl, Fisheries Branch, Department of Fisheries and Oceans, personal communication). Road access permitting surveillance from shore has helped Fishery Officers gather evidence. Sentencing has been strong with minimum fines of \$1,000 for first offenders and \$3,000 fines or gaol sentences for repeat offenders. Poaching in the area has decreased significantly since the rigorous enforcement began in 1979 (R. Kehl). Although poaching is suspected to be widespread in more remote areas such as the Queen Charlotte Islands and the west coast of Vancouver Island, the level of its intensity is unknown and likely to remain so.

A commercial northern abalone fishery also occurs in southeastern Alaska. The current regulations for the Alaska and British Columbia fisheries are compared in Table 11. Rationale for the British Columbia regulations will be given in the next section. The major difference is that entry is limited in British Columbia and the quota evenly distributed among licence holders. In Alaska between 1964 and 1974, the 9 yr with landings averaged 1.9 t annually (T. Koeneman, Alaska Dept. Fish. and Game, Petersburg). Landings from the commercial fishery in Alaska are compared with the British Columbia landings between 1975 to 1985 in Fig. 17. The Alaskan fishery experienced a rapid rise in landings to a maximum of 167 t in 1981, 3 yr after the peak British Columbia landings, and subsequently declined. There is no commercial fishery for northern abalone in Washington State, Oregon, or California.

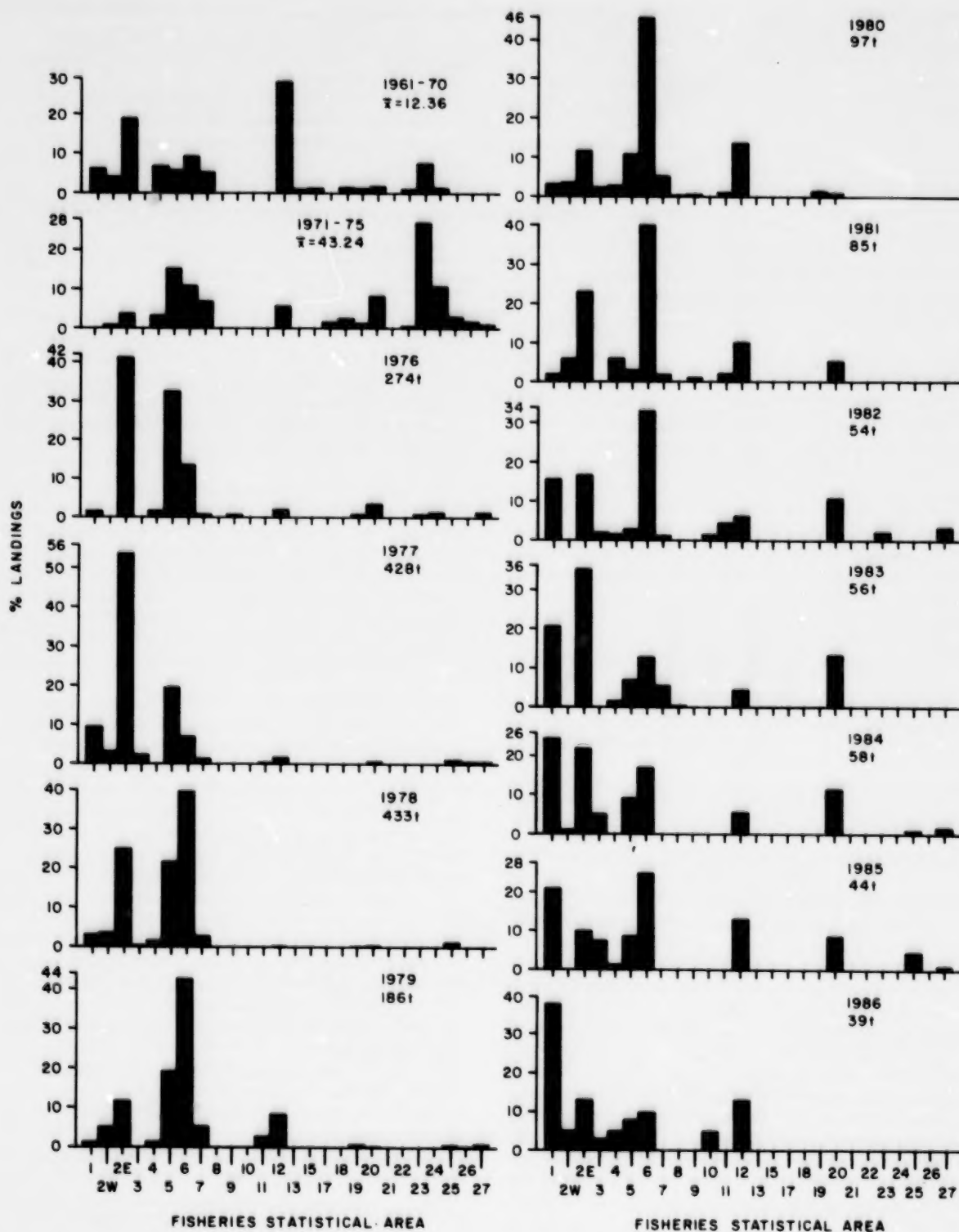


FIG. 16. Percentage landings of *Haliotis kamtschatkana* by Fishery Statistical Areas from 1961 to 1986. Illustrated are mean annual landings for 1961 to 1970 and 1971 to 1975; individual years 1976 to 1986 are shown separately (from Fedorenko and Sprout 1983, Farlinger and Bates 1985 and Fisheries Branch, Department of Fisheries and Oceans). Landings have never been reported from Fisheries Statistical Areas 14, 16, 28, and 29.

TABLE 11. Regulations for the commercial *Haliotis kamtschatkana* fisheries in Alaska and British Columbia for 1987. Alaskan data from T. Koeneman, Alaska Dep. of Fish and Game, Petersburg.

Jurisdiction	Limited entry Y/N (# of licences)	Closures (Y/N)		Legal size ^d (mm)	Quota (t)	Mandatory logs (Y/N)
		Area	Seasonal (dates/mo)			
Alaska	N ^a	Y ^b Y	May 16-Sept. 30/3.5	95 ^c	11.3 to 22.7 ^f in Ketchikan (Dall and Prince of Wales Is.); 3.6 in Sitka area (Baranof Is.)	Y ^a
British Columbia	Y (26)	Y ^c Y	Dec. 16-31, Jan. 1-15/1	100	47.2 coastwide	Y

^a Each diver must have a "fishing card" and each vessel must be licensed in which various area and any plan restrictions are stipulated. There is no limit on the number of licences.

^b Some areas closed to commercial operators, but all are open to "subsistence" harvesters (section 6.22).

^c List of closed areas issued each year to licence holders; closures occur in both north and south coasts.

^d Wording can be in maximum shell length or shell "diameter", which is equivalent.

^e Based on the belief that southeastern Alaska abalone are smaller overall than B.C. abalone (Livingstone 1952).

^f A "guideline harvest range" which varies according to management concerns, and quota not equally shared among licence holders as in B.C.

^g Harvesters provide a "fish ticket" with landings and sales information.

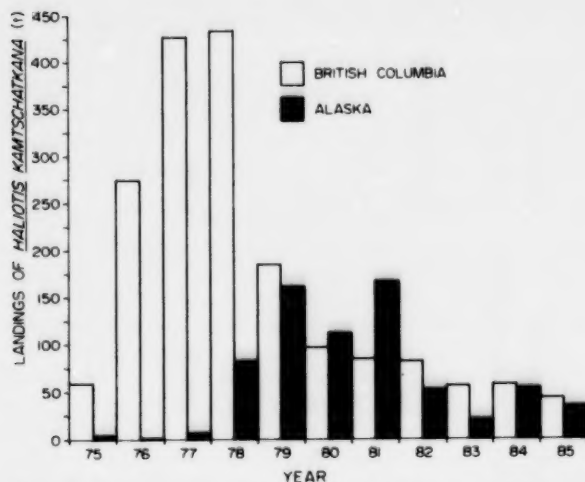


FIG. 17. Landings (in t live weight) of *Haliotis kamtschatkana* from southeast Alaska (data from T. Koeneman, Alaska Dep. of Fish and Game) and British Columbia from 1975 to 1985.

6.34 Commercial Fishery Management

A summary of regulations since 1972 concerning licences, quotas, legal sizes and season lengths is given in Table 10 and will be referred to throughout this section. Fedorenko and Sprout (1982) provide a comprehensive review of all early management, from 1952 to 1980.

Management of the fishery has had three phases. In the first phase, prior to 1976, the management philosophy was that a suitable minimum legal size would protect the fishery and no other regulation was required. The season was not closed, except that from 1911 to 1947 each third year was closed season. The reasoning behind this closure was not recorded. Lower Johnstone, Georgia, and Juan de Fuca Straits were all closed in 1971 to protect the recreational fishery, and Juan Perez Sound was closed in 1973 to protect native Indian and recreational fisheries. All other areas were open. Access to the commercial fishery was open to anyone with a personal fishing license and (after 1968) one of the unlimited 'C' licences. To obtain a 'C' licence one had only to have a vessel with an approved fish-holding space. During this first phase the

size limit changed twice. It began as 4" (101.6 mm) in total length in 1908. It was reduced to 3.5" (88.9 mm) in 1914, and then altered to 2.5" (63.5 mm) in shell width in 1938 (≈ 90 mm in shell length) and maintained until 1977.

The second management phase began in 1977. The marked rise in catches in 1976 created doubt about the efficiency of management by size limit alone. The California fishery, managed that way, experienced a sharp decline in landings beginning in 1970, and landings remained low through the early 1970's. This was blamed partly on sub-legal mortality caused by high fishing rates and partly on recruitment failure (Burge et al. 1975). Neither fishery managers nor biologists had an estimate of sustainable yield for northern abalone, but both considered the 1976 level too high. To keep the fishery under control and to prevent recruitment overfishing (Gulland 1973), managers made the decision to limit catches. The first step was to stop the 1976 fishery, which was closed in November. A meeting was held with abalone fishermen to discuss concerns and future options. A suite of regulation changes was made to rationalize the fishery and control catches. The major changes were:

- 1) Entry was limited to previous participants, resulting in 29 personal licences issued in 1977. They had participated in the fishery from 1975 to 1976.
- 2) Effort per licence was limited to three divers. Provision was made for divers to change during the season, but divers' names were listed according to licensee and registered with the licensing authority. This was intended to prevent day-to-day changes in diving rosters.
- 3) The season was reduced in length to 8 months from 1 April to 27 November.

These changes were all intended to limit catches. Further changes were:

- 4) The size limit was restored to 4" (101.6 mm) shell length (Table 10).
- 5) Several area closures were made for a variety of reasons (Fedorenko and Sprout 1982).
- 6) Regulations were made to govern harvesting procedures. Abalones were required to be measured underwater and replaced immediately if sub-legal.

- 7) As a condition of the licence, fishermen were required to submit logs showing, for each day fished: exact location of fishing, effort expended by each diver (hours), and catch taken by each diver.

These regulations failed to control the catch, which rose further to 428 t in 1977. Managers and biologists still had no estimate of a sustainable yield but agreed that the catch should be reduced to about 255 t. The 1978 season was reduced to only three months, 1 March - 31 May. This action also failed — the 1978 catch was 433 t.

Limiting entry does not limit catch (Pearse 1982). This point is driven home by the behaviour of this fishery. Breen and O'Halloran (1987) suggest that the management strategy of limiting entry may even have caused fishing effort to increase. By the end of 1978, an estimate of sustainable yield, albeit a crude one, was available (Breen 1980b). This was that 113.4 t could be taken on a sustainable basis from the Areas open in 1976.

In 1978 the decision was made to manage the fishery by setting explicit quotas, and the third phase of management began in 1979. Three additional decisions were made at this point. First, the overall quota of 113.4 t was phased in, with a quota of 226.8 t for 1979 and 113.4 t for 1980 (Table 10). Second, managers divided the total quota in each year equally among licence holders. This system was the first on the Pacific coast of Canada. The rationale provided by Fedorenko and Sprout (1982) was that boat-quotas: "attempted to accommodate operators of small vessels which lacked freezing facilities, and to provide for local fresh markets, both of which would have been seriously impaired by a short, open fishery. The regulations also supported the Minister's policy of providing some protection to the operators of small vessels, many of whom pioneered the fishery." Third, the 1979 season was divided into two parts: a short 'scramble' season for 113.4 t followed by a second season in which the remaining 113.4 t was divided evenly among licence holders. The first season ended when the quota was taken in 18 days. The second season was nearly 7 mo long, since with individual quotas there was no further need to restrict season length. Neither was there a need for a minimum landing requirement, and it was revoked. Restrictions on the number of divers per vessel were removed the next year.

The 1980 season proceeded according to the plan. For 1981, however, the quota was reduced to 94.3 t. This reduction was made for several reasons. The fishery was operating in a considerably smaller area than the one which supported the sustainable yield estimate. Illegal handling practices causing sublegal mortality had been observed. Most seriously, it was now clear that recruitment of juveniles to many populations was failing, although probably not as a result of fishing pressure. Breen (1984) recommended further decreases based on examination of the assumptions used in the original analysis.

Since 1981, managers have continued to decrease the annual quota in reaction to declining abalone abundance. A quota of 47.2 t has been in effect from 1985 through 1987. Some areas closed to commercial fishing have been re-opened, for instance parts of the west coast of Vancouver Island in 1987.

In 1977 entry was limited to 29 harvesters as a special category of the previously unlimited general C licence for small inshore fisheries. In order to qualify, harvesters had to have either landed an excess of \$2000 worth of abalone or made at least 50 % of their fishing income from abalone. The licence was, and still is, "personal" and non-transferable. Initially the licensee could only report landings from a vessel in which he was a majority owner. A performance criterion of 2.3 t landed annually was required as necessary for licence renewal, although this condition was removed after the 1978 season. From the outset there was no "operator restriction" so a licensee did not have to fish abalone personally. This made possible the eventual leasing of fishing privileges mentioned below. By 1978 the abalone licence became a special E licence exclusive to abalone and a final number of 26 was set in 1979 (Table 10). In time, some of the original licence holders stopped harvesting and some leased from other licence holders the right to harvest and land abalone under the original licensee's name. This evolved further in that some original licensees have granted Power of Attorney to lessees who fish, and report all harvesting activities directly to Fisheries and Oceans on their own behalf. This aided fleet reduction (Table 10). Fifteen vessels in 1985 reported landings from the 26 licences. Some individuals now have numerous leases and a vessel may report landings from up to 5 licences. The original intent of ensuring access to the fishery for pioneering harvesters is now less relevant with many original licensees not harvesting. Changes such as moving licence rights to active harvesters and imposing an operator restriction so that licences are actually worked by licensees will be topics of future management discussions.

6.35 Stock Assessment

No stock assessment was carried out on northern abalone in British Columbia until the suddenly intensified fishery in 1976 created a serious need. Before 1976, the work of Quayle (1971) provided a good estimate of growth rate, information about the reproductive cycle, and population size structures. No information existed on mortality or recruitment rates, on total stock abundance, or sustainable yields.

It is not practical to estimate total stock size from resource surveys (section 5.21). Breen (1980b) estimated change in abalone abundance from 1976 to 1978 based on several methods. He compared densities measured at seven stations in 1976 or 1977 and again in 1978. The relative abundance of legal sized abalones between Quayle's (1971) samples and those of Breen and Adkins (1979) were compared under the assumption that the abundance of sub-legal abalones had not changed in order to estimate change in legal abalone abundance. Finally, an estimate of pre-fishery abundance was made from anecdotal sources. These three methods indicated that the stock had declined by 60-90 % in harvested parts of the north coast.

Breen (1980b) then used growth and mortality estimates to examine annual productivity, which appeared to be 6.5 % of the original standing stock. He used estimates of original density, stock reduction, catches and produc-

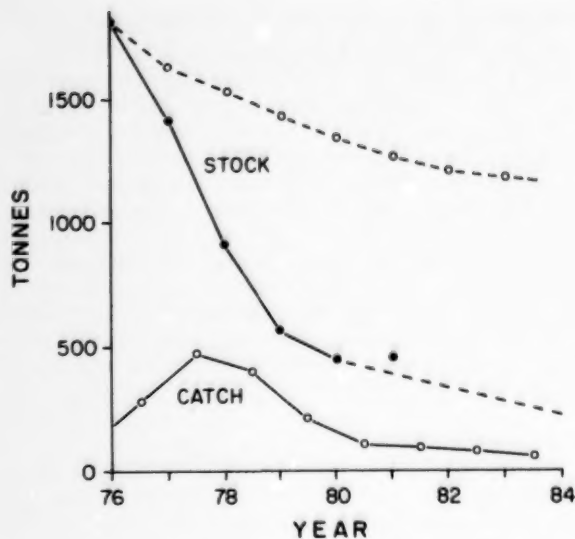


FIG. 18. A British Columbia *Haliotis kamtschatkana* stock reconstruction based on a stock reduction solution. The solution was obtained with $M=0.20$, $P=0.25$, $B_0=1800$ t, using landings from 1976 to 1980 (from Breen 1986). $P=B_n/B_0$ where B_n is biomass at year n .

tivity in a primitive stock reduction analysis to estimate that sustainable yield from an equilibrium population would be 113 to 155 t annually. This estimate depended on several important assumptions outlined in 1978 and examined subsequently (Breen 1980b; Breen and Adkins 1981; Boutillier et al. 1985). It was necessary to assume that recruitment was constant, that sub-legal mortality caused by fishing was negligible, and that no habitat change was caused by fishing. Later, it became clear that the first assumption was incorrect; recruitment was not stable (section 5.3).

The stock reduction method of Kimura and Tagart (1982; see also Kimura et al. 1984 and Kimura 1985) was used by Breen (1986). This uses the vector of catches, estimated stock reduction, and estimated M . It assumes constant recruitment (at least in this version) and simultaneously estimates virgin biomass and yearly values of F . With $M=0.20$, no plausible solution could be found where recruitment was sufficient to replace the virgin population. It was concluded that recruitment from 1975 to 1983 must have been less than the replacement level. This supports the direct estimates of recruitment (section 5.3) and is consistent with observations of population size structure (section 5.13).

A stock reconstruction from stock reduction analysis is shown in Fig. 18. In this result, the pre-fishery biomass (January 1975) was estimated as 1800 t; the stock was reduced to 450 t by the end of 1980. Estimated F values from 1976 to 1980 were 0.18, 0.46, 0.66, 0.51, and 0.30 respectively. Using the estimated recruitment level over this period, the stock would have declined to about 1200 t by 1980 even in the absence of fishing.

Yield-per-recruit (YPR) analysis was performed for *H. kamtschatkana*, using the parameters $M=0.20$, $K=0.25$ and $L_\infty=130$ mm. The Beverton and Holt

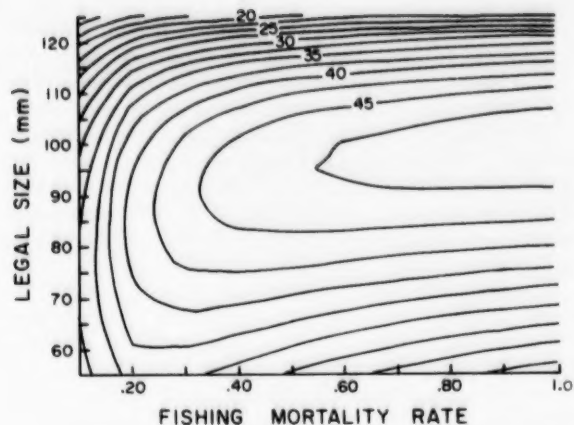


FIG. 19. Yield-per-recruit (g) in British Columbia *Haliotis kamtschatkana* as a function of minimum legal size and instantaneous fishing mortality rate (F), determined with the method of Beverton and Holt (Ricker 1975). Parameters were $M=0.20$, $K=0.25$, $L_\infty=130.0$ mm. W_∞ was determined from length-weight relations for *H. kamtschatkana* in Breen and Adkins (1982) (from Breen 1986).

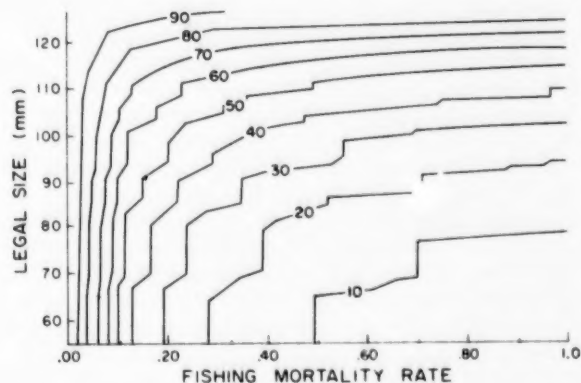


FIG. 20. Eggs-per-recruit of British Columbia *Haliotis kamtschatkana* expressed as a percentage of the eggs produced by an unfished cohort (from Breen 1986). See text for procedure. Parameters were all identical to those used in Fig. 19.

(1957) yield isopleths (Fig. 19) show that the present minimum legal size of 100 mm is optimal, especially if F is high. If F was still 0.30, as estimated for 1980, a size limit of 90 mm would give slightly better YPR.

A problem with YPR analysis is that fishing may influence subsequent recruitment. The relation between stock and recruitment is almost never available, but recruitment overfishing is an obvious danger when high F is combined with a small minimum legal size. This can be examined by conducting egg-per-recruit (EPR) analysis, which is simple simulation modelling to determine the equilibrium egg production implied by various combinations of F and size limit. The result is expressed as a percentage of egg production in the virgin population. For abalone, this method was first used by Sluczanowski (1984).

Figure 20 shows the results of EPR analysis for *H. kamtschatkana*, using the same growth and mortality

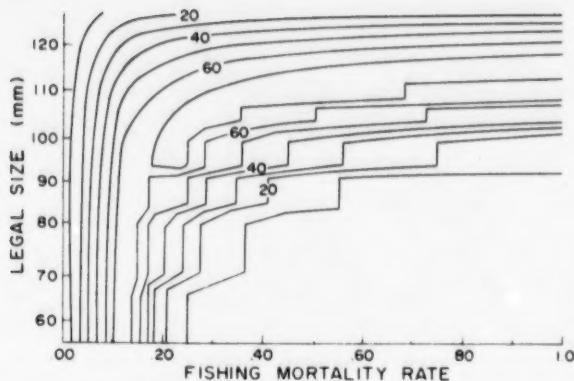


FIG. 21. Relative values of various combinations of minimum legal size and fishing mortality rate of British Columbia *Haliotis kamtschatkana*, using the procedure described in the text (from Breen 1986). Values have a range of 0 to 100; 100 represents maximum yield-per-recruit and at least 50 % egg production.

parameters as for Fig. 19. The assumed fecundity curve was given in section 4.15. At levels of F estimated above, the present minimum size limit (100 mm) should have ensured egg production rates at 35–50 % of the virgin population rate. These rates are higher than those from which recruitment overfishing might be expected to result.

Results from YPR and EPR can be combined. Breen (1986) suggested that where egg production rates are above 50 %, a manager should have no worry about future recruitment. Rates below 20 % are probably too low for safety. He assigned value of 1 to situations yielding rates above 50 %, a value of 0 to rates < 20 % and a linear intermediate value to rates between 20 and 50 %. He then multiplied this value by the yield-per-recruit (expressed as a percentage of the maximum value) to obtain a relative "strategy value" for that combination of F and minimum legal size. The result for northern abalone, combining the data in Fig. 19 and 20, is shown in Fig. 21. The present size limit is optimal if $F \leq 0.20$; at higher F a size limit of 110 mm would be more suitable, and this size is optimal to very high values of F .

These analyses use growth, mortality and fecundity relations that are assumed to apply to the whole population. It has been shown that growth rates vary greatly among populations in different habitats; mortality rates and fecundity curves are likely to vary also. This kind of analysis should be repeated when more is known about population dynamics of northern abalone in different habitats.

For abalone populations elsewhere, the most common stock assessment tool has been YPR analysis. Examples based on the Beverton-Holt method include Isibasi and Kojima (1979) for *H. discus discus*; Harrison (1983) and Sluczanowski (1984, 1986) for *H. laevigata* and *H. rubra*, Clavier and Richard (1985) for *H. tuberculata* and Tegner et al. (1988) for *H. rufescens* and *H. corrugata*. Sainsbury (1977, 1982b) developed his own age-structured model to estimate yield-per-recruit in *H. iris*.

Surplus production analysis, based on the method originally developed by Schaefer (1954), has been carried

out only for Australian species by Harrison (1983) and Sluczanowski (in Lewis et al. 1984). The latter reviewed the problems of trying to use this kind of model for abalone. These include the long lag between spawning and recruitment (often longer than the data series length), problems with standardizing effort, the poor relation between CPUE and stock size, and the distribution patterns of abalone. He concluded that "traditional models which deal with catch and effort data offer almost no guidance for managers of the abalone fishery until more data are available."

Kojima et al. (1978) used daily catch records to estimate catchability and F with DeLury's method (Ricker 1975). This method is subject to some of the same problems as surplus production analysis: effort is difficult to standardize and CPUE may be misleading in abalone fisheries (section 5.22).

Prince et al. (1987) argue, from an experimental removal of *H. rubra*, that dispersal is extremely limited in *Haliotis* larvae. The applicability of their result to other species has yet to be examined. If it is general, the form of stock-recruit relations could be determined relatively easily in abalone.

6.36 Surveys

Although northern abalone surveys did not start until 1976, there are some previous anecdotal reports. Thompson (1914) reported abalone observations made incidentally during a Province-wide intertidal clam survey. Only on the Queen Charlotte Islands and at Port Neville on the mainland coast were abalone "very abundant", although he suggested that abalone occurred along all outer coasts such as the west coast of Vancouver Island. Quayle (1962) recounted a 1955 survey by a California "hard hat" diver in the Hecate Strait area. Populations were considered too patchy and sparse to warrant a hard hat-style fishery in that area. Better knowledge on the occurrence of local stocks was coming from SCUBA divers and Quayle (1962) proposed that fishery potential would be best realized by mobile SCUBA divers able to access local concentrations. Between 1955 and 1970, Quayle (1971) visited 14 locations coastwide (Fig. 22).

Figures 23 and 24 illustrate the approximate coastal areas of the 14 surveys between 1976 and 1987. The north coast has dominated sampling effort as it has dominated landings (section 6.32); only one south coast survey has been reported. The sample methods, results and general conclusions of the surveys are summarised in Table 12. The standard density estimation technique, which has remained in use since, was first used in the fifth survey, in August 1978 (Breen and Adkins 1979). The technique covers an area of 7 m × 16 m, generally larger than the scale of local abalone aggregations and was described by Breen and Adkins (1979) as follows: "The 16 quadrats were arranged in four transects, each 4 m apart; and each of the four quadrats within a transect were 1 m apart. The first quadrat was located as randomly as possible at the top or bottom of the habitat to be surveyed, and the transects ran up and down the vertical slope. If there was no slope, the direction of the first transect was chosen randomly, and then the pattern was followed."

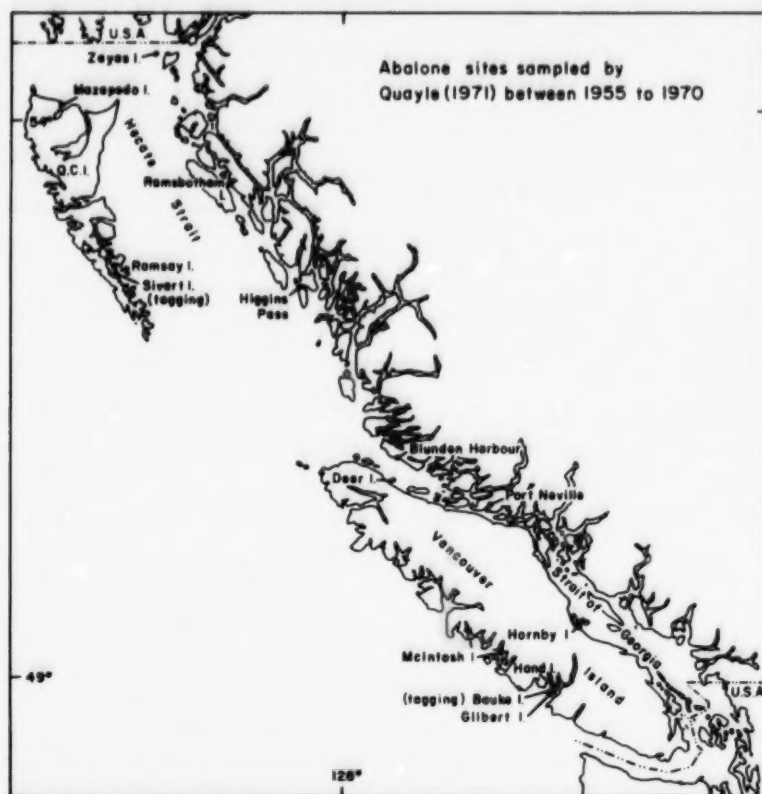


FIG. 22. *Haliotis kamtschatkana* collection sites between 1955 and 1970 (from Quayle 1971).

Sixteen 1 m² quadrats were chosen because they generated acceptable confidence limits and could be completed with reasonable diving effort, $\approx$ 0.5 tank of air per diver per locality. Alternate quadrats were used because of autocorrelation in densities in adjacent quadrats. Initially, rocks were not turned within the quadrats and thus juveniles were knowingly underestimated, but juvenile sampling did occur at some sites. By the seventh survey, in April to July of 1979 (Breen and Adkins 1981), all boulders were turned within the quadrats. Boutillier et al. (1985) compared density when all loose boulders in the quadrats were turned. In the 1984 survey, cryptic abalone searches increased overall density counts by $\approx$ 25 % and legal densities by $\approx$ 11 % compared to counting just exposed abalone.

The 16-quadrat method was used to compare densities in specific areas with previous densities. When densities have declined by large amounts, the method is powerful enough to demonstrate statistical significance (e.g. Boutillier et al. 1984, 1985). However, the technique is not inherently strong for use in this way (see Breen and Adkins 1981). To show a real 25 % decline from a mean density of 1.0 m⁻² at one site would require that at least 100 quadrats be counted both times. This is based on the mean/variance ratio given by Breen (1980b). New sampling designs will be required to demonstrate future changes.

In addition to the sampling problem caused by natural variation, problems in re-locating previously sampled sites

increase sampling error still further. Breen and Adkins (1981) suggested that a series of permanently identifiable benchmark sites be established to overcome this.

A persistent criticism of density estimates obtained in surveys was that biologists chose the sites. Fishermen argued that higher estimates would have been obtained had they chosen the sampling locations. This was tested by Boutillier et al. (1985), who found no difference between the mean density at sites previously selected and sites chosen by a commercial fisherman. Beginning in 1979, some sites were sampled more intensively for unbiased samples of the whole population size structure (section 5.13).

6.4 Changes in Abundance

The first comparative examination of abundance was made by Breen (1980b) (section 5.23), who used several methods to estimate that density decreased 60-90 % in harvested areas of the north coast from 1976 to 1978. This estimate was a rough one. It depended partly on anecdotal estimates of pre-fishery abundance and partly on the assumption that sub-legal densities in populations sampled by Quayle (1971) were the same as those sampled later. Where it compared measured densities, the areas sampled were small.

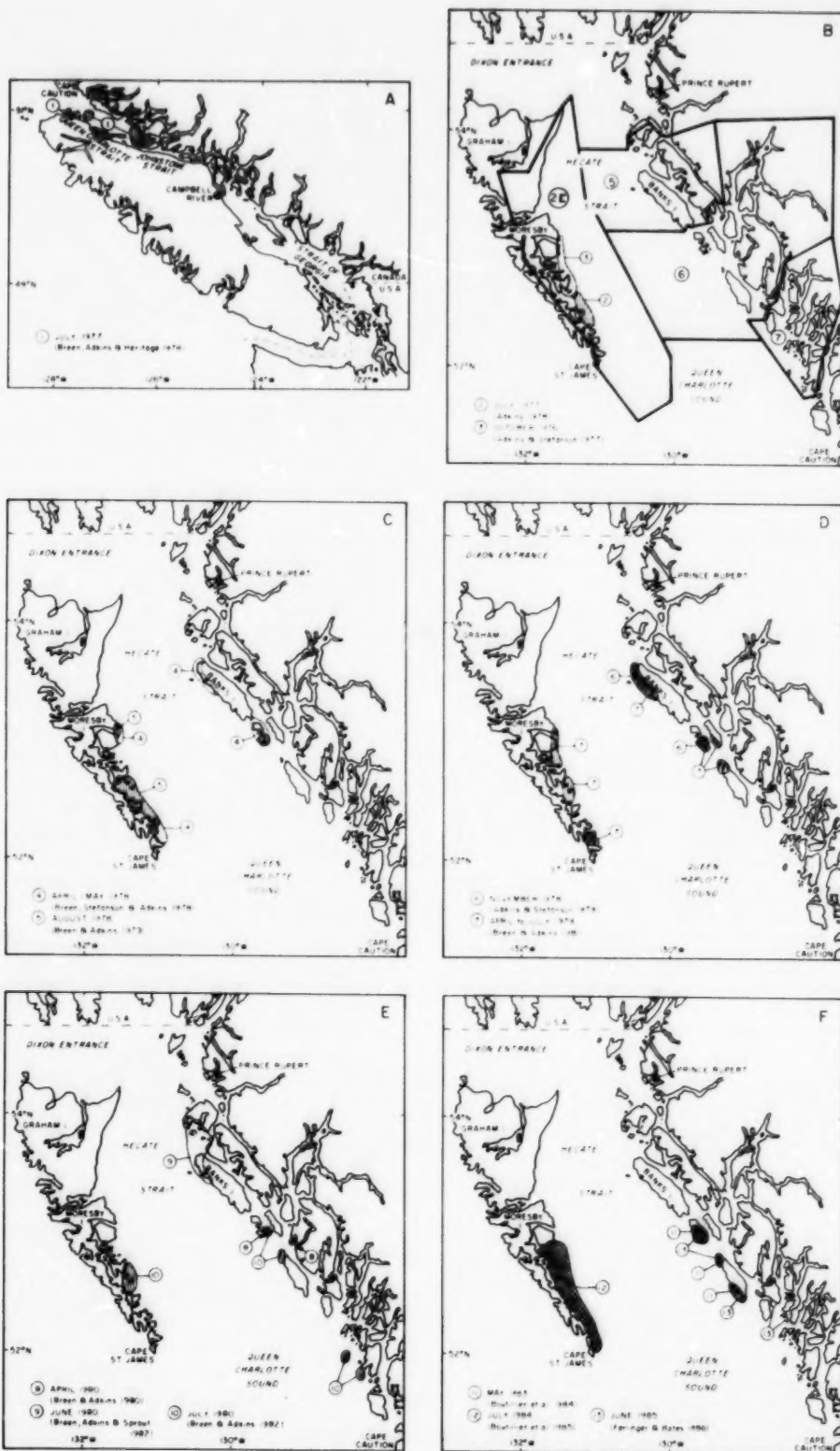


FIG. 23. Approximate localities of *Haliotis kamtschatkana* surveys in British Columbia between 1976 and 1985 reported in the literature. Fishery Statistical Area 2E, 5, 6, and 7 boundaries shown in B.

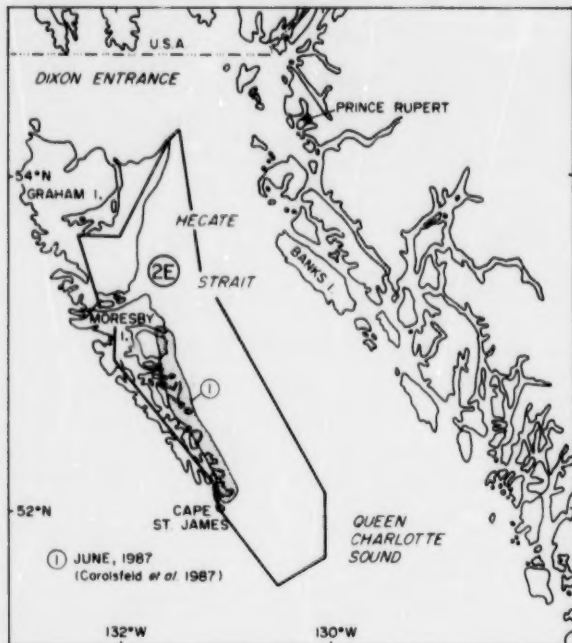


FIG. 24. Approximate locality of the *Haliotis kamtschatkana* survey in the southeast Queen Charlotte Islands (Fishery Statistical Area 2E) in June 1987.

Better estimates of changes in abundance were made by Boutillier et al. (1984, 1985), who visited previously surveyed places and made new density estimates. From 1979-80 to 1983 in eastern Hecate Strait, density of legal-sized abalone decreased by 45-55% and total density decreased by 30%. From 1978 to 1984 in the southeast Queen Charlotte Islands, density of legal-sized abalone decreased by 75% and total density by 81%. In the latter survey, the same decrease occurred in areas open and closed to commercial fishing (Table 12).

In a further survey of eastern Hecate Strait in 1985, Farlinger and Bates (1986) examined sites with highest densities in the 1983 survey. They found no significant difference in the mean density of legal sized abalone, total density, or new recruit and pre-recruit densities. In a 1987 survey of western Hecate Strait, Carolsfeld et al. (1987) also found no significant difference in mean abalone density (legal, total, new-recruit, prerecruit), since the 1984 survey reported by Boutillier et al. (1985) (Table 12). Both sides of Hecate Strait show no recent decrease in abalone abundance, albeit at a significant lower level overall than recorded in surveys of the late 1970's.

The simplest explanation for the declines reported by Boutillier et al. (1984, 1985) would be that commercial fishing decreased the numbers of legal-sized abalones. Because of the high potential fishing power of divers (Beinssen 1979; Murray 1982) this is undoubtedly a partial explanation, but explains neither declines in sub-legal abalone nor declines in areas closed to commercial fishing.

Declines in sub-legal abalone are consistent with information presented above. Size frequency distributions indicate that some populations are not being replaced by

juvenile settlement (section 5.13). Pre-recruits and new recruits in 1978 and subsequently were less abundant than required to maintain the virgin population (section 5.3). Stock reduction analysis (section 6.35) also indicates that recruitment was lower than replacement levels for 1975 to 1980.

Boutillier et al. (1985) argue that declining settlement and recruitment are probably not a result of the fishery. A scarcity of juveniles was present in 1976 samples, which could not have been affected by the fishery. From settlement to recruitment requires at least 6 yr, thus any impact on recruitment from the intense 1976-1978 fishery should not have been detected until 1984. Finally, EPR analysis does not support the idea that recruitment over-fishing has occurred (section 6.35). The apparent recruitment failure cannot, therefore, be blamed on the commercial fishery. It is possible that recruitment may be affected by low stocks since 1980 (Fig. 18).

It is possible that settlement in *H. kamtschatkana* fluctuates independently of the parental stock. Direct and indirect environmental effects on spawning, settlement and survival may cause fluctuation. Abalone do not necessarily spawn each year (e.g. Sainsbury 1982a). Temperature appears to be a major controlling influence on spawning (section 4.16), so yearly variation in temperature regime could cause irregularity in fecundity, spawning times and larval survival (section 4.21). It is suggestive that, in the northern abalone populations examined in 1978 and 1980 (Breen and Adkins 1979, 1982), juvenile abundance was greatest in *Pterygophora* and least in *Macrocystis* forests. The former are exposed; the latter tend to be found in more sheltered situations.

In some marine invertebrates, favourable conditions for settlement may be rare. Paine (1986) observed that the sea urchin *Strongylocentrotus purpuratus* settled successfully only 4 times in 20 yr on the outer Washington coast, and suggested that settling success was associated with warm water events. Shepherd et al. (1985) suggest that poor settlement of *H. scalaris* is associated with cool water temperatures. Similar suggestions are made by Hayashi (1980b) and Forster et al. (1982) to explain fluctuations in *H. tuberculata*.

An indirect effect of hydrographic events is suggested by Sakai (1962), who found a high correlation between abalone landings and harvests of the seaweed *Undaria pinnatifida*. Sakai suggests that seaweed growth, and consequently abalone production, varies with the strength of the Kurile current.

The declines observed by Boutillier et al. (1985) in areas closed to commercial fishing might have been caused by poaching, recreational fishing or unusually high adult mortality such as a rapid disease episode. There is, as yet, no way to exclude these explanations. Breen (unpublished observations) observed a dramatic decrease in abundance at Hoskins Islet, within the Juan Perez Sound closure, between 1980 and 1981. At this site, most individuals were sublegal. Quayle (1971) observed unexplained disappearances of northern abalone at Sivart Island in Juan Perez Sound and Nanoose Bay in Georgia Strait. Some possible causes of adult mortalities are discussed in section 4.34.

From lamentably meagre evidence, one can speculate that historical abundance of *H. kamtschatkana* varied

TABLE 12. Sample methods, results and conclusions of surveys for northern abalone, *Haliotis kamtschatkana*, in British Columbia, 1976 to 1987.

Author(s)	Date (M/Y)	Localities	Dive Sites	Sample methods and effort	Purpose, major results, and conclusions
Adkins, and Stefanson (1977)	10/76	Fig. 23B	11	- at each site a 1 m wide transect 10 to 15 m long and parallel to shore at 2 to 6 m depth. - at each site 100 to 300 abalone measured; length frequencies (LF), $n = 800$. - substrate and biota notes taken at each site.	- exploratory survey with density and size structure measurements. - by comparing nearby fished and unfished areas, alleged harvesting decreases of $\approx 1 \text{ m}^{-2}$ from original densities of 5 to 10 m^{-2}. - no change in mean abalone sizes at fished sites. - most exposed sites had the smallest mean sizes. - first mention of potential competition between sea urchin and abalone.
Breen, Adkins and Heritage (1978)	07/77	Fig. 23A	34	- all sites dived to 10 m below chart datum with substrate and biota noted. - quadrats used at one site only, otherwise abalone abundance was "estimated visually". - LF, $n = 450$	- exploratory survey. - speculated that any sites with relatively high abundance had been missed by fishermen. - initial landings were of "accumulated stock" and any sustainable yield should be less than the high initial yields because of slow adult growth and low recruitment. - Port Neville population unique in apparently being isolated and self sustaining with predicted rapid post-harvest recovery characteristics.
Adkins (1978)	07/77	Fig. 23B	5	- at each site 3 to 5 one m wide transects perpendicular to shore were made. - transects were 5 to 15 m long and lay between upper and lower limits of abalone distribution. - exposure, substrate and biota of each site noted. 50 abalone were measured per site; LF, $n = 270$.	- to obtain density measurements in harvested and unharvested areas. - alleged harvested sites had mean densities of 0.9 to 1.7 m^{-2} compared to 4.4 m^{-2} in an apparently unfished site. - mean abalone size smaller at the most exposed site, only 5% legal sized compared to >50% legal sized at all other sites. - abalone length frequencies illustrated for each site.
Breen, Stefanson and Adkins (1978)	04-05/78	Fig. 23C	21	- sites had been previously harvested. "visual estimates" of abalone densities made at each site. - substrate and biota notes taken at LF taken at each site of 60 to 264 abalone; $n = 2550$. - under-rock and crevice searches for juveniles at some sites.	- exploratory survey and size structure measurements. - mean % legal size per site was 65.1 (range 0-100). - estimated densities ranged from 0 to 10 m^{-2} with a mean of 2.0 m^{-2}. - the first survey in which juveniles were specifically searched for.
Breen and Adkins (1979)	08/78	Fig. 23C	131	- the first report using the conventional 16 m^2 method (section 6.36). - this method used at most sites, har vest history of sites recorded. - each site described for substrate and biota. - juveniles counted at some sites by searching cryptic habitats. - at 43 sites LF samples taken; $n = 3850$.	- to obtain density and size structure estimates in an extensive survey of harvested and unharvested sites. - first mention of relation between habitat type and abalone size and abundance (see section 3.22). - mean size, and production potential varies between sites, first mention of the term "surf abalone" for small adults from exposed habitats. - juveniles occur deeper than adults and are underestimated in counts because of their cryptic habits. - sea urchins speculated to invade areas harvested of abalone.
Adkins and Stefanson (1979)	11/78	Fig. 23D	13	- used 16 m^2 method at previously harvested sites (1977, 1978). - each site described for substrate and biota. - all abalone seen were measured; LF, $n = 450$.	- to obtain density and size structure estimates in harvested areas of eastern Hecate Strait. - site descriptions with mean densities, % legal and density of legal-sized abalone. - results intended for detailed analysis in Breen (1980b). - mean site densities ranged from 0.6 to 5.0 m^{-2} and mean % legal = 47%.
Breen and Adkins (1981)	04-07/79	Fig. 23D	58	- used 16 m^2 method and turned over all rocks to find cryptic abalone at some sites. 11 sites intensively ('stratified') sampled using continuous transects from chart datum until no abalone were encountered, all rocks turned for cryptic abalone; 27 to 158 m^2 per site ($\bar{x} = 78 \text{ m}^2$). - at sites with low densities, thorough non-quadrat searches were completed. 2 300 abalone collected by "haphazard swimming" at 2 sites, measured and tagged. - some of the sites had been surveyed in 1978.	- to compare densities with previous years' densities; to review abundance estimates and population structure; to carry out tagging for growth studies; to intensively sample sites for size frequencies. 16 m^2 quadrat method used at 1978 and 1979 sites did not show differences in % legal sized abalone. - criticized 16 m^2 method as a tool for assessing sites over time (section 6.36). - discussed problems with estimating recruitment (section 5.3) and abalone productivity. - reviewed goals for later field work: improve estimates of sustainable yields by improving on uncertainties in growth and recruitment by recovering tags and sampling entire vertical range for juveniles.

TABLE 12. (cont'd)

Author(s)	Date (M/Y)	Localities	Dive Sites	Sample methods and effort	Purpose, major results, and conclusions
Breen and Adkins (1980b)	04/80	Fig. 23E	12	16 m² quadrat method at sites with appreciable numbers, all rocks overturned. 1 site intensively sampled with continuous 1 m wide transects 17-25 m long. - low density sites had "subjective estimates" only. - habitat notes made at each site. - LF taken; n = 520.	- exploratory survey. - estimated productivity of a good commercial bed (legal density 0.68 m⁻²). - discussed the wide confidence intervals around legal densities from quadrat counts where real changes in abundance would be difficult to estimate from quadrat counts (section 6.36).
Breen, Adkins, and Sprout (1982)	06/80	Fig. 23E	43	16 m² quadrat method used at 8 sites, all abalone measured, all rocks overturned. - low density sites had visual observations only. - habitat notes made at each site. - LF, n = 1200.	- to examine distribution and abundance of abalone in an area where native Indian food fishing was important. 13 sites suitable for intertidal picking, i.e. native Indian 'food fishing', according to access and occurrence. 13 sites suitable for commercial harvest according to legal densities. 7 sites suitable for both, which could be areas of potential conflict over the resource
Breen and Adkins (1982)	07/80	Fig. 23E	20	16 m² quadrat method used when abalone density was sufficient, all rocks overturned. - all abalone from quadrats measured; LF, n = 3200. - visual observations only in low density sites. 1100 abalone tagged at one site. 6 sites were chosen for intensive 'stratified' sampling: 2 of which had been harvested, 2 <i>Nereocystis</i>, 1 <i>Macrocystis</i>, 1 <i>Pterygophora</i>; abalone were taken from 3 zones at each site: shallow kelp zone/10 m seaward of kelp zone/deepest 'lower' zone; abalone numbers, lengths, widths, heights, sex, and weights were recorded from each zone.	- to explore the Goose Island group for abalone; continue tagging abalone; recover abalone tagged in 1979; intensively sample whole population at 6 sites for size frequency data and morphometric analysis. - the largest and most abundant abalone were in the shallow kelp zone. - marked between-site variation in recruitment (section 5.3). - marked between-site variation in morphometrics (section 4.4). - tag recovery rates very poor after 1 year, between 1.6% and 3.9%. 64 abalone recovered from the 2 300 tagged in 1979 (Breen and Adkins 1981).
Boutillier et al. (1984)	05/83	Fig. 23F	42	16 m² quadrat method used at 40 sites (2 had too few abalone), all rocks overturned. - habitat notes made at all sites; LF n = 1070. - tried to resample sites sampled by Breen and Adkins (1980, 1981, 1982) but accuracy only within ~100 m of original sites. - sampled.	- to measure density and size structure at previously surveyed sites and to estimate change. - overall abalone abundance had decreased from previous surveys, as had % legal and prerecruit abundance 45 to 55% decline in legal densities. - density of pre-recruits (94-101 mm) and new recruits (102-107 mm) decreased by 50 to 56% in Area 6. - suggested that observed stocks would be ~15 to 20% of prefishery levels. - suggested rehabilitation measures, such as closures, for Areas showing poor recruitment. - no difference between densities at sites chosen by biologists and fishermen.
Boutillier et al. (1985)	07/84	Fig. 23F	70	16 m² quadrat method used at 60 sites (10 sites had too few abalone for this method). - all rocks in quadrats were overturned to find cryptic abalone. - habitat notes made at all sites; LF, n = 730. - some sites had been previously sampled in 1978 and 1980 (Breen and Adkins 1980, 1981, 1982). - new sites chosen after discussion with fishermen.	- to measure density and size structure at previously sampled sites for estimation of population change. - a comparison of 1978-79 sites revisited in 1984 (n=61) revealed a 75% decline in legal abalone. - entire population decline of 81%, stock suggested as being "not in equilibrium". - localities open and closed to the commercial fishery both showed significant stock declines from 1978 to 1979 levels.

TABLE 12. (cont'd)

Author(s)	Date (M/Y)	Localities	Dive Sites	Sample methods and effort	Purpose, major results, and conclusions
Farlinger and Bates (1986)	06/85	Fig. 23F	28	16 m² quadrat method used at all sites, all rocks in sample quadrats overturned. 25 sites selected for comparison with habitat notes made at all sites; LF, n = 700.	- to measure density and size structure at previously sampled sites for estimation of population change; to respond to industry reports of increased legal densities. - in 25 sites, mean total densities increased from 1.43 m⁻² in 1933 to 1.57 m⁻² in 1985 and mean legal densities increased from 0.23 to 0.35 m⁻², respectively. - abundance of pre-recruits and new recruits did not change from 1983 to 1985. - no significant abalone population change in the survey area since 1983. - first stock survey not showing appreciable declines in abalone abundance.
Carolsfeld et al. (1988)	06/87	Fig. 24	77	16 m² quadrat method used at all sites, all rocks in sample quadrats overturned. - the same 70 sites of 1984 in Boutillier et al. (1985) sampled plus 7 new sites. - habitat notes made at all sites; LF, n = 832.	- to resurvey the sites reported in Boutillier et al. (1985) to measure density and population structure. - in 63 comparable sites between 1984 and 1987 no significant changes in mean densities of total, legal, pre-recruit, or new recruit abalone. - no significant difference between densities in areas open to the fishery or closed, between 1984 and 1987 (63 sites used in comparison). - no decline in stock abundance since 1984, but stocks still significantly lower ($\bar{x}$ total density of 0.75 m⁻²) than 1978-79 surveys in the same area (57 sites used in 1978-79, 1984 and 1987 in comparison).

considerably. Thompson (1914) searched for abalone with a "water glass" but gave no direct estimate of abundance. He states:

"It is in sufficient numbers at present to allow canning, and free use by local residents. In certain localities a man armed with suitable implements may easily gather several sackfuls at each low tide."

In 1955, an exploratory survey was made by a hardhat diver (Quayle 1962) at 26 locations in the area later examined by Breen and Adkins (1979). The survey found no abalone at 8 sites, a "few" at 4 sites, and a mean of 8 at the remaining 14 sites (D. B. Quayle, pers. comm.). This result contrasts markedly with later observations. Breen and Adkins (1978) found a much smaller proportion of sites with no abalones, an overall mean density of 2.5 m⁻², and a legal density of 0.58 m⁻². If the 1955 diver was accurate, then northern abalone must have been very much less abundant in the southeastern Queen Charlotte Islands in 1955 compared with 1914 and 1978.

6.5 Transplantation for Improved Growth

Emmett et al. (1988) reported on a northern abalone transplant experiment in Barkley Sound (Statistical Area 23) on the west coast of Vancouver Island. They evaluated the potential for enhancing growth of stunted "surf" abalone (section 4.43) by transplanting them to more sheltered sites. Sublegal abalone < 100 mm (n = 5414) were removed from an exposed shore, measured, and 1011 (18.7 %) tagged. All were transplanted to two more sheltered sites with *Macrocystis* forests. Two other sites with their resident abalone were used as controls, first an exposed surf abalone site (n = 454 measured and tagged)

and second a transplant control site (n = 457 measured and tagged) similar in shelter characteristics to the two receiving sites. At a third control site, 377 resident abalone were tagged and monitored for movement. All five sites had been surveyed beforehand for abalone density, % legal-sized, topography, algal cover, and abalone predators and competitors.

After nine months, they harvested tagged abalone from control sites and tagged and untagged abalone from the transplant sites. The tagged:untagged ratio of the samples was similar to the initial ratio (1:5). Tag recovery at the transplant sites was 38 and 71 %. Significant growth had occurred at all sites. Growth at the two transplant sites was significantly greater than at the surf abalone control site. Post-handling mortality was $\approx$ 2 to 3 % and overall losses were attributed to predation rather than emigration.

Emmett et al. (1988) concluded:

- 1) transplanting sublegal-sized abalone was biologically feasible and best done with larger sublegals
- 2) site criteria (topography, algal food, predators, past history of abalone presence) were important as recovery rate will vary greatly between sites
- 3) transplant procedures (< 3 h emersion, handling, predator control, are important
- 4) transplants could be economically feasible depending on labour costs and recovery of legal-sized abalone.

Assuming it would take two years for an 85 mm abalone to reach 100 mm, a 30 % recovery rate of legal abalone was suggested as possible after a carefully run transplant operation. Vasserot (1983) suggested that *H. kamtschatica* would be a suitable species to transplant north of the present range of *H. tuberculata* in Europe, such as southern Norway, Eire and Scotland.

7. Mariculture

The hatchery technology for mariculture of abalone has been developed mostly in Japan (Mottet 1978; Uki 1984) and California (McCormick and Hahn 1983; Ebert and Houk 1984; Hooker and Morse 1985). The ocean ranching of hatchery-raised abalone seed, released at ≈ 25 mm shell length, has been widespread throughout northern Japan (Saito 1984). Moreover, considerable energy is expended by the Japanese on habitat enhancement in aid of abalone productivity (Mottet 1980, 1981). Harrison (1986) points out that after 12 yr, in which 5 million seed abalone were released annually, Japanese catch statistics have not appreciably increased. However, increases have been observed in some areas (Inoue 1983). Japanese workers are apparently concerned most about seed mortality, but reasons for their limited success remain unknown. Harrison (1986) suggested that understanding the parental stock-recruitment relationship would be vital to the success of an abalone reseeded campaign.

The survival of two size groups (45 and 71 mm) of red abalone (*H. rufescens*) seed released in southern California was $\approx 1\%$, with 43% losses through mortality and some significant proportion to emigration (Tegner and Butler 1985b). Predation limited the success of seeding and nearly continuous predator control would be necessary to improve survivorship. Tegner and Butler (1985b) suggested that until the variables of predation and alleged emigration became better understood, the viability of red abalone reseeded was doubtful.

Since the late 1970's, Pacific Trident Mariculture Ltd. of Victoria, B.C. has employed Japanese and Californian abalone culture technology on *H. kamtschatkana*. Calderwood (1985) reviewed their results, obtained between 1982 to 1985 under a Department of Fisheries and Oceans contract. A hatchery and field growout system for northern abalone culture was outlined, along with detailed recommendations for hatchery design. They proposed a three phase culture system:

- 1) Hatchery production (1-yr-olds)
- 2) Intermediate culture (1- and 2-yr-olds)
- 3) Growout system (3-yr-olds)

Another northern abalone culture program, also based on Japanese and California technology, was undertaken from 1978 to 1983 at the Washington State Department of Fisheries Point Whitney Shellfish Laboratory (Olsen 1984). Their work extended from brood stock manipulation to 4 yr of growout in "semi-field conditions" of open raceways in a green house-type enclosure. The following text outlines only the various steps applied from the pre-existing technology to northern abalone culture; specific details and literature references can be found in Olsen (1984) and Calderwood (1985).

Calderwood (1985) detailed results in three phases as follows:

PHASE 1

Phase 1 (hatchery production) produces 1-yr-old "seed" abalone and is the most technical and costly.

a) Maturation of adults

Adult brood stock is harvested from wild stock in January. Each animal is weighed, measured, indexed for gonad maturation, and tagged. They are then placed in conditioning tanks where temperature and photoperiod are manipulated to ensure optimal gonad maturation conditions. Olsen (1984) found that best conditioning occurs at 10–12°C for 2–3 wk in Spring followed by a gradual increase to 13–14°C.

b) Induction of spawning

When the brood stock have reached sexual maturity (May/June), spawning of the separated sexes is induced by exposure to either a high dosage of ultraviolet light and temperature shock or a 250 ppm solution of hydrogen peroxide (H_2O_2) buffered with TRIS (tris(hydroxymethyl) aminomethane) to pH ≈ 9.1 (Olsen 1984). Spawning can be induced year round although adequate survival past metamorphosis to the benthic stage only occurred in the summer-autumn period (Olsen 1984).

c) Fertilization

Eggs are siphoned from the female tank to produce one layer of eggs on the bottom of a disinfected aquarium. Sperm density of water from the male tank is determined with a haemocytometer and sperm is mixed with eggs to a final concentration of 400 000 mL⁻¹. Ultraviolet-sterilized seawater is used throughout fertilization and larval culture. Olsen (1984) held 10–100 sperm per egg for 10–15 min before washing the eggs.

d) Washing the eggs

All excess sperm are rinsed from the aquarium to reduce possible bacterial contamination by allowing the eggs to settle to the bottom and decanting the water, refilling and repeating the process several times.

e) Hatching

The fertilized eggs are held at a constant temperature until hatching, at which time the trochophore larvae are active swimmers. The larvae are not disturbed until complete formation of their larval shells.

f) Larval culture

The two methods are:

i) Static system — the larvae are held in a small tank and the water changed $\approx$ every 8 h by carefully pouring the delicate larvae into a screened ($\approx 40 \mu\text{m}$) chamber and rinsing them into a tank of fresh seawater.

ii) Flow-through system — here a chamber is made of 20.3 cm (8") diameter PVC pipe, 35.6 cm (14") deep with screening on the bottom. This chamber is held in a container with the water level lower than the height of the chamber. A water flow of 200 mL $\cdot$ min⁻¹ is introduced at the top of the chamber. A chamber undergoes a complete water change and sterilization every 24–48 h.

g) Larval settlement

i) Preparation of corrugated PVC plates and cultivation of benthic diatoms — The plates are held in a vertical position suspended in a seawater raceway receiving natural sunlight; a film of benthic diatoms settles naturally. When an appreciable diatom film appears, the plates are grazed by introduced 1-yr-old abalone. They graze most of the large diatoms leaving behind a community of smaller diatoms suitable for ingestion by larvae. When the plates have been well grazed for approximately 1 wk, they are ready for larval settlement.

ii) Settlement — When larvae are ready for settlement, prepared plates are placed horizontally into a tank. Larvae are then distributed evenly throughout the tank. When the larvae have settled on the plates, water flow and aeration commences. Stages (a) to (g) take place in heated ($\approx 12^{\circ}\text{C}$) seawater and subsequent stages in ambient temperature seawater. Gamma amino butyric acid (GABA) was used effectively to stimulate larval metamorphosis.

h) Intensive larval culture

After settlement, the plates are removed from the settlement tanks and placed in long raceways receiving constant water flow, aeration and natural sunlight. Diatom growth is controlled with shading. As the juveniles grow and consume a larger quantity of diatoms from the plates, sunlight is increased. Olsen (1984) defined individuals as juveniles after the appearance of the shell's first respiratory pore. This occurred after 2.5–3 mo (in $9\text{--}13^{\circ}\text{C}$) at a shell length of 0.8–1.8 mm.

i) Preparation for intermediate culture

At an age of ≈ 9 to 12 mo, juveniles are transferred into a net cage where they are fed a kelp diet of *Macrocystis integrifolia* and *Nereocystis luetkeana*. The juveniles are held for 2–3 mo. New shell growth from a kelp diet is easily discernible as a change in colour from red to emerald green occurs (Olsen 1968). Olsen (1984) transferred juveniles to open tanks at 28 wk (≈ 7.5 mm shell length).

PHASE 2

Phase 2 (intermediate culture) takes 'seed' abalone through to their second year.

a) Site location

The site chosen should offer the following:

- (i) good water quality
- (ii) relatively fast water currents
- (iii) kelp food source easily accessible
- (iv) shelter from rough weather conditions.

Where the water currents are relatively fast, it is possible to house a larger number of abalone per artificial habitat.

b) Deep water lease

Required by Provincial Government for any off-bottom culture.

c) Kelp harvesting licence

Required by Provincial Government for a specific area, volume and kelp species.

d) Selection of artificial habitat

Habitats can range from concrete to PVC pipe. A system using 204.6 L (45 gal) polyethylene barrels perforated with 9.5 mm ($3/8''$) holes capable of holding 1 500 1-yr abalone each, was deployed in an area with good currents.

e) Float design

A recommended float style for the barrel habitats is a 3.6×9.1 m ($12' \times 30'$) planked platform with three 2.4 m ($8'$) square holes in the deck. Each hole would allow twelve polyethylene barrels to be suspended from a cross beam. This system enables use of 36 barrels housing in excess of 60 000 juveniles in a 33.4 m^2 (360 ft^2) area.

f) Feeding and cleaning cycle

The habitat should be raised weekly, rinsed out and kelp replaced with a fresh supply. Once every second or third month fouling should be removed from the outside of the barrels, although this should be adjusted according to site and season.

PHASE 3

Phase 3 (growout) in the natural environment for the on-growing of 2 yr-old abalone was not attempted during the study (Calderwood 1985), although the following were suggested:

a) Site location

An underwater survey is required to select a site with good water quality and sufficient rocky substrate providing a combination of kelp feeds.

b) Subtidal lease and transplant permit

A lease is definitely required for the growout site from the Provincial Government and a permit from the Federal Government is necessary to transplant abalone stock to the site.

c) Predator and competitor control

Predators (sea stars, crabs, octopus) and competitors (sea urchins) should be regularly removed during growout.

d) Artificial habitats

Should the site not have a rocky substrate, it would be possible to install an artificial habitats such as 2 m (6') concrete culverts or 1.5 m (5') high domes. Diatoms and kelp should grow on the habitats prior to transplant of stock. This system would be advantageous over a sandy substrate to reduce migration of transplants by effectively creating islands of firm substrate.

e) Food cultivation

Growout sites without adequate kelp must be supplemented either by on site kelp culture or harvesting from other areas to provide feed.

f) Three/four-year culture.

During this growout period, the major task is feeding and regular monitoring. Bimonthly dives should be made to control predators and competitors. The abalone should experience a annual growth rate of ≈ 18 mm, provided they are well fed. In their growout, Olsen (1984) reported a first year mean shell length of 22 mm with a range of 8 to 32 mm according to various holding protocols. Mean lengths for the next 3 yr were 37, 59, and 69 mm, respectively. By age 3 gonads appeared mature and by age 4 some abalone spawned. Overall survival was $\approx 70\%$ over 3 yr among abalone > 10 mm long.

Calderwood's (1985) summary of accomplishments in *H. kamtschatkana* culture was:

- 1) broodstock maturation stimulated through manipulation of water temperature.
- 2) spawning reliably induced through ultraviolet irradiation of seawater or hydrogen peroxide treatment
- 3) preparation of settlement substrate refined, chemical settlement inducers used, and optimal larval stage for settlement determined
- 4) benthic diatoms and macroalgal fragments evaluated as dietary components during intensive juvenile culture
- 5) California red abalone (*H. rufescens*) readily spawned and hybrid larvae (*rufescens* $\times$ *kamtschatkana*) survived to 1-mo after settlement, although disease outbreaks prevented further evaluation.

8. Recommendations for Future Northern Abalone Research

H. kamtschatkana appears to be reasonably similar to other *Haliotis* species in basic life history characteristics. Much of what is known about other *Haliotis* species is relevant to northern abalone and no striking or unique aspect of the biology of northern abalone has been discovered. Nevertheless, there are major gaps in our knowledge of northern abalone.

This is particularly true in the field of basic natural history. For example, influences on mortality of early life stages are unknown and the diet of all stages in nature has yet to be examined. In many cases, no laboratory work exists as the basis for speculation about what happens in

the field. We suggest, for instance, that salinity, temperature, exposure to wave action and availability of juvenile substrate may determine the horizontal and vertical distributions of northern abalone within British Columbia. Information about temperature tolerances is very limited and comes from Alaska, while there is no information on salinity tolerances or tolerances to water movement. Some simple work would be extremely valuable in interpreting distribution patterns.

Small-scale distribution patterns have not been studied, except to establish vertical patterns. It is known that abalones are contagious when examined in 1 m^2 quadrats, and that densities change markedly over short distances. Nothing about scales of aggregation is known. If the ideas of Prince et al. (1987) are correct, such scales will need to be understood in order to manage the fishery properly.

Virtually nothing is known about short-term movement patterns. The issue of how abalones forage, and how that behaviour is influenced by abalone size, presence of predators and abundance of food, is a potentially rewarding question for study. Similarly, while one can speculate that sea urchins are a potential competitor, this question can only be studied properly with basic laboratory observations and replicated field manipulations. The answer to this question has both general ecological importance and relevance to fishery management. Both species are the targets of commercial fisheries: how does the fishery for one affect the biology of the other?

From a fisheries research standpoint, the most obvious avenue for further work is to address the process of recruitment to the population. Two extreme alternatives are as follows. First, settlement and survival of juveniles could be largely independent of the breeding stock, and population dynamics might be characterized by periodic pulses of high settlement produced by a small breeding stock. If this were so, the poorly understood history of population abundance in the species (section 6.37) would be explained. If this alternative prevails, the sensible strategy for a fishery manager is to extract the best discounted cash flow from strong cohorts when they appear, without considering EPR.

The other extreme possibility is suggested by recent Australian work. Prince et al. (1987) suggest that dispersion of larvae is extremely limited, so that local populations must be managed as separate stocks. A suggestion emerges from some studies that juvenile settlement is correlated with breeding biomass or egg production (Sluczanowski 1984; Prince et al. 1987). This pattern may then be modified by environmental influences on breeding success and survival of the early life stages. In this situation, the goal of management becomes complex — a question of trying to balance good egg production with good fishery yield; and trying to maintain the resource in the face of future environmental uncertainty (Walters 1975; Ludwig 1980).

To distinguish between these alternatives requires that breeding stocks and settlement rates be carefully monitored at a variety of sites. The breeding stock is comparatively low, so such monitoring is especially important now. Just as important is replicated experimental manipulation of breeding adult abundances, to test the ideas of Prince et al. (1987).

As part of the same question, fecundity and reproductive success should be examined in this species. No direct estimates of size-specific fecundity have yet been made. It is probable that egg production is influenced by local conditions, especially temperature, exposure and food quality and availability. This should be examined to determine whether parts of the whole population are more important to the reproductive process than others. For instance, "surf" abalone are currently not harvested. It is important to know whether they are important to the total reproductive activity of the stock.

Some of the studies suggested would require areas to be protected from exploitation. If significant northern abalone life history work is to be done, it would be important to develop scientific reserves. Finally, commercial catch sampling, for use in determining exploitation rate, should be carried out regularly on a scale that allows valid inferences to be drawn.

9. Acknowledgments

Thanks to B. Adkins, W. Carolsfeld, K. Hobbs, T. Shields and many others for assistance in the field and with the abalone data base over the years. We are most grateful to Drs. R. J. Beamish and G. S. Jamieson for their support at the Pacific Biological Station which made this project possible. B. Adkins, J. Boutillier, S. Farlinger and G. S. Jamieson reviewed the manuscript and provided many comments. Carol Roy and the Word Processing Unit provided excellent assistance. Tim Koeneman (Alaska Department of Fish and Game, Petersburg), L. Goodwin (Washington State Department of Fisheries, Point Whitney) and D. O. Parker (California Department of Fish and Game, Long Beach) very kindly supplied information on their abalone fisheries. Dr. Susan Bower and G. Calderwood advised us on diseases and northern abalone mariculture. Special thanks to Dr. Dan Quayle (Pacific Biological Station), Dr. Mia Tegner (Scripps Institution of Oceanography) and Scoresby Shepherd (South Australian Department of Fisheries) for sharing their abalone experience and unpublished information with us, and their painstaking reviews of earlier drafts.

10. References

- ADKINS, B. E. 1978. An examination of some commercially harvested abalone populations in the Moresby Island area. Fish. Mar. Serv. MS Rep. 1455: 19 p.
- ADKINS, B. E. AND A. P. STEFANSON. 1977. An examination of harvested and unharvested abalone populations in the Moresby Island area. Fish. Mar. Serv. MS Rep. 1435: 23 p.
1979. North coast abalone survey in harvested areas, November 1978. Fish. Mar. Serv. MS Rep. 1500: 15 p.
- BARGMANN, G. G. 1984. Recreational diving in the State of Washington and the associated harvest of food fish and shellfish. Wash. State Dep. Fish. Tech. Rep. 82: 59 p.
- BATES, K. T. 1984. Review of the 1982 commercial abalone fishery in British Columbia. Can. MS Rep. Fish. Aquat. Sci. 1749: 22 p.
1985. Review of the 1983 commercial abalone fishery in British Columbia. Can. MS Rep. Fish. Aquat. Sci. 1826: 25 p.
- BEAUDRY, C. G. 1983. Survival and growth of the larvae of *Haliotis kamtschatkana* Jonas at different temperatures. J. Shellfish Res. 3: 109-110.
- BEINSSSEN, K. 1979. Fishing power of divers in the abalone fishery of Victoria, Australia. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 175: 20-22.
- BEINSSSEN, K. AND D. POWELL. 1979. Measurement of natural mortality in a population of black-lip abalone, *Notohalotis ruber*. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 175: 23-26.
- BERNARD, F. R. [ED.]. 1982. Assessment of invertebrate stocks off the west coast of Canada (1981). Can. Tech. Rep. Fish. Aquat. Sci. 1074: 39 p.
- BEVERTON, R. J. H., AND S. J. HOLT. 1956. A review of estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 140: 67-83.
1957. On the dynamics of exploited fish populations. U.K. Min. Agric. Fish. Food, Fish. Invest. (Ser. 2) 19: 1-533.
- BIGG, M. A. AND I. B. MACASKIE. 1978. Sea otters re-introduced in British Columbia. J. Mammal. 59: 874-976.
- BOUTILLIER, J. A., W. CAROLSFELD, P. A. BREEN, AND K. T. BATES. 1984. Abalone survey in the Estevan group and Aristazabal Island, May 1983. Can. MS Rep. Fish. Aquat. Sci. 1747: 60 p.
- BOUTILLIER, J. A., W. CAROLSFELD, P. A. BREEN, S. FARLINGER, AND K. T. BATES. 1985. Abalone resurvey of the southeast Queen Charlotte Islands, July 1984. Can. MS Rep. Fish. Aquat. Sci. 1818: 87 p.
- BOWER, S. M. 1986. The life cycle and ultrastructure of a new species of thraustochytrid (Protozoa: Labyrinthomorpha) pathogenic to small abalone. Abstract in: 2nd Int. Colloq. Pathol. Mar. Aquat., Portugal.
- 1987a. *Labyrinthuloides haliotidis* n. sp. (Protozoa: Labyrinthomorpha), a pathogenic parasite of small juvenile abalone in a British Columbia mariculture facility. Can. J. Zool. 65: 1996-2007.
- 1987b. Pathogenicity and host specificity of *Labyrinthuloides haliotidis* (Protozoa: Labyrinthomorpha), a parasite of juvenile abalone. Can. J. Zool. 65: 2008-2012.
- BREEN, P. A. 1980a. Muscled mollusc: the northern abalone. Diver 6(6): 26-28.
- 1980b. Measuring fishing intensity and annual production in the abalone fishery of British Columbia. Can. Tech. Rep. Fish. Aquat. Sci. 947: 49 p.
- 1980c. The ecology of red sea urchins in British Columbia. Proc. First Int. Symp. Coastal Pacific Marine Life, Washington State University, October 1979; p. 3-12.
1984. Recommendations for the 1983 abalone season, p. 53-56. In: G. S. Jamieson [ed.]. 1982 shellfish management advice, Pacific Region. Can. MS Rep. Fish. Aquat. Sci. 1774.
1986. Management of the British Columbia fishery for northern abalone (*Haliotis kamtschatkana*), p. 300-312. In: G. S. Jamieson and N. Bourne [ed.]. North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.
- BREEN, P. A. AND B. E. ADKINS. 1979. A survey of abalone populations on the east coast of the Queen Charlotte Islands, August 1978. Fish. Mar. Serv. MS Rep. 1490: 125 p.
- 1980a. Spawning in a British Columbia population of northern abalone, *Haliotis kamtschatkana*. Veliger 23: 177-179.
- 1980b. Observations of abalone populations in Emily Carr Inlet and Lotbinière Bay, April 1980. Can. MS Rep. Fish. Aquat. Sci. 1576: 17 p.

1981. Abalone surveys and tagging conducted during 1979. Can. MS Rep. Fish. Aquat. Sci. 1623: 88 p.
1982. Observations of abalone populations on the north coast of British Columbia, July 1980. Can. MS Rep. Fish. Aquat. Sci. 1633: 55 p.
- BREEN, P. A., B. E. ADKINS, AND G. D. HERITAGE. 1978. Observations of abalone and subtidal communities made during a survey of the Queen Charlotte Strait and upper Johnstone Strait areas July 13-20, 1977. Fish. Mar. Serv. Tech. Rep. 789: 91 p.
- BREEN, P. A., B. E. ADKINS, AND P. E. SPROUT. 1982. Abalone populations on the west coast of Banks Island, June 1980. Can. MS Rep. Fish. Aquat. Sci. 1640: 42 p.
- BREEN, P. A., T. A. CARSON, J. B. FOSTER, AND E. A. STEWART. 1982. Changes in subtidal community structure associated with British Columbia sea otter transplants. Mar. Ecol. Prog. Ser. 7: 13-20.
- BREEN, P. A. AND D. A. FOURNIER. 1984. A user's guide to estimating total mortality rates from length frequency data with the method of Fournier and Breen. Can. Tech. Rep. Fish. Aquat. Sci. 1239: 63 p.
- BREEN, P. A. AND S. O'HALLORAN. 1987. The British Columbia abalone fishery. Catch (M.A.F., Wellington, New Zealand) 14(1): 22-23.
- BREEN, P. A., A. P. STEFANSON, AND B. E. ADKINS. 1978. North Coast abalone surveys in harvested areas, spring 1978. Fish. Mar. Serv. MS Rep. 1480: 61 p.
- BURGE, R., S. SCHULTZ, AND M. ODEMAR. 1975. Draft report on recent abalone research in California with recommendations for management. California Dep. Fish and Game, CA. 62 p. (Mimeo)
- CALDERWOOD, G. 1985. Technological advances in the field of abalone mariculture. Final Prep. (1982-1985) Pacific Trident Mariculture Ltd. Victoria, B. C., 125 p. Contract to Dep. of Supply and Services, Canada, No. 053B. FP 501-2-005.
- CALDWELL, M. E. 1981. Spawning, early development, and hybridization of *Haliotis kamtschatkana* Jonas. M.Sc. thesis, University of Washington, Seattle, WA. 55 p.
- CARMICHAEL, J. R. AND N. BOURNE. 1986. Proposed techniques for the assessment of recreational invertebrate harvest in British Columbia. Can. MS Rep. Fish. Aquat. Sci. 1869: 30 p.
- CAROLFELD, W., S. FARLINGER, B. C. KINGZETT, N. A. SLOAN, AND G. THOMAS. 1988. Abalone resurvey in the southeast Queen Charlotte Islands, June 1987. Can. MS Rep. Fish. Aquat. Sci. 1966: 95 p.
- CLAVIER, J. 1982. [Initial data on natural ormer (*Haliotis tuberculata*) stocks in the Saint Malo Region.] Association pour la mise en valeur du littoral de la Côte d'Emeraude, Study Report. 100 p. (Translated from French by Can. Transl. Fish. Aquat. Sci., No. 4928, 1983).
- CLAVIER, J., AND O. RICHARD. 1984. Etude expérimentale du déplacement de l'ormeau (*Haliotis tuberculata*) dans le milieu naturel. Rev. Trav. Inst. Pêches Marit. 46: 315-326.
1985. Etudes sur les ormeaux dans la région de Saint-Malo. Association pour la mise en valeur du littoral de la Côte d'Emeraude, France, 285 p.
- 1986a. Growth of juvenile *Haliotis tuberculata* (Mollusca: Gastropoda) in their natural environment. J. Mar. Biol. Assoc. U.K. 66: 497-503.
- 1986b. Estimation du stock naturel d'ormeau (*Haliotis tuberculata*) dans la région de Saint-Malo. Rev. Trav. Inst. Pêches Marit. 48: 95-105.
- COCHARD, J.-C. 1980. [Research on factors determining sexuality and reproduction in *Haliotis tuberculata* L.] Doctoral thesis, University of Western Brittany. 162 p. (Transl. from French by Can. Transl. Fish. Aquat. Sci., No. 4946, 1983.)
- COWAN, T. MCT., AND C. J. GUIGUET. 1965. The mammals of British Columbia, 3rd ed. B.C. Prov. Mus. Handb. No. 11: 414 p.
- COX, K. W. 1962. California abalones, Family Haliotidae. Calif. Dep. Fish Game Fish. Bull. 118: 133 p.
- DALZELL, K. E. 1973. The Queen Charlotte Islands. Vol. II. Of places and names. Dalzell Books, Prince Rupert, B.C. 125 p.
- DAYTON, P. K., AND M. J. TEGNER. 1984. Catastrophic storms, El Niño, and patch stability in a southern California kelp community. Science 224: 283-285.
- DOI, T., S. A. GUZMAN DEL PROO, V. MARIN ACEVES, M. ORTIZ QUINTILLANA, J. CAMACHO ACOSTA, AND T. MUNOZ LOPEZ. 1977. Analisis de la poblacion y diagnostico de la pesqueria de abulon amarillo (*Haliotis corrugata*) en el area de Punta Abreojos e Islas Cedros, B.C. Direccion. General del Instituto Nacional de Pesca, Serie Cientifica 18: 17 p.
- EBERT, E. E., AND J. N. HOUK. 1984. Elements and innovations in the culture of red abalone, *Haliotis rufescens*. Aquaculture 39: 375-392.
- ELSTON, R., AND G. S. LOCKWOOD. 1983. Pathogenesis of vibriosis in cultured juvenile red abalone, *Haliotis rufescens* Swainson. J. Fish. Dis. 6: 111-128.
- EMMETT, B., H. I. MCELDERRY, AND G. S. JAMIESON. 1988. An experimental transplant of prerecruit abalone in Barkley Sound, British Columbia. Fish. Bull. (In press).
- ESTES, J. A., AND G. R. VAN BLARICOM. 1985. Sea-otters and shellfisheries, p. 187-235. In: J. R. Beddington, R. S. H. Beverton, and D. M. Lavigne [eds.] Marine mammals and fisheries. Allen & Unwin, London.
- FARLINGER, S. AND K. T. BATES. 1985. Review of shellfish fisheries in northern British Columbia to 1984. Can. MS Rep. Fish. Aquat. Sci. 1841: 35 p.
1986. Abalone survey in the Estevan group and Aristazabal Island, June 1985. Can. MS Rep. Fish. Aquat. Sci. 1896: 45 p.
- FEDORENKO, A. Y., AND P. E. SPROUT. 1982. Abalone biology, fishery regulations, commercial catch (1952-1980), and current state of resource in British Columbia. Can. MS Rep. Fish. Aquat. Sci. 1658: 74 p.
- FORSTER, G. R. 1967. The growth of *Haliotis tuberculata*: Results of tagging experimentation Geurmsey 1963-65. J. Mar. Biol. Assoc. U.K. 47: 287-300.
- FORSTER, G. R., G. W. POTTS, AND R. SWINFEN. 1982. Changes in the ormer populations of Guernsey and Jersey. J. Mar. Biol. Assoc. U.K. 62: 717-727.
- FOSTER, M. S., AND D. R. SCHIEL. 1985. The ecology of giant kelp forests in California: A community profile. U.S. Fish Wildl. Serv. Biol. Rep. 85(7.2): 1-152.
- FOURNIER, D. A., AND P. A. BREEN. 1983. Estimation of abalone mortality rates with growth analysis. Trans. Am. Fish. Soc. 112: 403-411.
- GARLAND, C. D., S. L. COOKE, J. F. GRANT, AND T. A. MCMEEKIN. 1985. Ingestion of the bacteria on and the cuticle of crustose (non-articulated) coralline algae by post-larval and juvenile abalone (*Haliotis ruber* Leach) from Tasmanian waters. J. Exp. Mar. Biol. Ecol. 91: 137-149.
- GIORGI, A. E., AND J. D. DEMARTINI. 1977. A study of the reproductive biology of the red abalone, *Haliotis rufescens* Swainson, near Mendocino, California. Calif. Fish Game 63: 80-94.
- GULLAND, J. A. 1973. Can a study of stock and recruitment aid management decisions? Rapp. P.-V. Réunion. Cons. Int. Explor. Mer 164: 368-372.
1983. Fish stock assessment-A manual of basic methods. FAO/Wiley Series on Food and Agriculture, Vol. 1. J. Wiley and Sons, Chichester and New York, 223 p.

- HARRISON, A. J. 1983. The Tasmanian abalone fishery. *Tasmanian Fish. Res.* 26: 44 p.
1986. Gastropod fisheries of the Pacific with particular reference to Australian abalone, p. 14-22. In G. S. Jamieson and N. Bourne [ed.]. *North Pacific Workshop on stock assessment and management of invertebrates*. Can. Spec. Publ. Fish. Aquat. Sci. 92.
- HARRISON, A. J. AND J. F. GRANT. 1971. Progress in abalone research. *Tasmanian Fish. Res.* 5: 1-10.
- HARTWICK, B., L. TULLOCK, AND S. MACDONALD. 1981. Feeding and growth of *Octopus dofleini* (Wulker). *Veliger* 24: 129-138.
- HAYASHI, I. 1980a. The reproduction biology of the ormer, *Haliotis tuberculata*. *J. Mar. Biol. Assoc. U.K.* 60: 415-430.
- 1980b. Structure and growth of a shore population of the ormer, *Haliotis tuberculata*. *J. Mar. Biol. Assoc. U.K.* 60: 431-437.
1983. Seasonal changes in condition factors and in the C:N ratio of the foot of the ormer, *Haliotis tuberculata*. *J. Mar. Biol. Assoc. U.K.* 63: 85-95.
- HINES, A. H., AND J. S. PEARSE. 1982. Abalones, shells and sea otters: Dynamics of prey populations in central California. *Ecology* 63: 1547-1560.
- HOLM, W. 1965. Northwest coast Indian art. An analysis of form. Thomas Burke Memorial Washington State Museum Monograph 1. University of Washington Press, Seattle, WA. 115 p.
- HOOKE, N., AND D. E. MORSE. 1985. Abalone: the emerging development of commercial cultivation in the United States, p. 365-414. In J. V. Huner and E. E. Brown [ed.]. *Crustacean and mollusk aquaculture in the United States*.
- INO, T. 1951. American *Haliotis kamtschatkana* and the far-eastern *Haliotis kamtschatkana*. *Bull. Biogeog. Soc. Jpn.* 15: 39-41.
1953. Biological studies on the propagation of Japanese abalone (genus *Haliotis*). Tokyo Univ. Fish., Tokai Publ. Co., 108 p.
1966. [The abalone science and its propagation in Japan.] Nippon Suisan Shigen Hogo Kyokai, Suisan Zoyoshoku Soshu 11: 104 p. (Transl. from Japanese by Fish. Res. Board Can. Transl. Ser. No. 1078, 1968.)
- INOUE, M. 1983. Effect of stocking with cultured fish larvae in the coastal waters of Kanagawa Prefecture. *Bull. Jap. Soc. Sci. Fish.* 43: 69-70.
- ISIBASI, K., AND H. KOJIMA. 1979. [A study on the stock of Japanese black abalone, *Haliotis discus discus* in Tokushima Prefecture — III. Analysis on abalone fisheries management.] *Bull. Tokai Reg. Fish. Res. Lab.* 98: 65-75. (Transl. from Japanese by Can. Transl. Fish. Aquat. Sci. No. 4866, 1982.)
- JAMIESON, G. S. 1986. A perspective on invertebrate fisheries management — the British Columbia experience, p. 57-74. In: G. S. Jamieson and N. Bourne [ed.]. *North Pacific Workshop on stock assessment and management of invertebrates*. Can. Spec. Publ. Fish. Aquat. Sci. 92.
1988. Status of the northern abalone, *Haliotis kamtschatkana*, in Canada. *Can. Field Nat.* (In press).
- JOHNSON, C. R., AND K. H. MANN. 1986. The crustose coralline alga, *Phymatolithon foliis*, inhibits the overgrowth of seaweeds without relying on herbivores. *J. Exp. Mar. Biol. Ecol.* 96: 127-146.
- KIM, J.-W., AND S.-C. CHUNG. 1985. On the growth of abalones, *Sulcalus diversicolor diversicolor* (Reeve) and *S. diversicolor aquatilis* (Reeve), in Cheju Island. *Bull. Mar. Resour. Res. Inst. Cheju Nat. Univ.* 9: 39-50.
- KIMURA, D. K. 1985. Changes to stock reduction analysis indicated by Schnute's general theory. *Can. J. Fish. Aquat. Sci.* 42: 2059-2060.
- KIMURA, D. K., J. W. BALSIGER, AND D. H. ITO. 1984. Generalized stock reduction analysis. *Can. J. Fish. Aquat. Sci.* 41: 1325-1333.
- KIMURA, D. K., AND J. V. TAGART. 1982. Stock reduction analysis, another solution to the catch equations. *Can. J. Fish. Aquat. Sci.* 39: 1467-1472.
- KOJIMA, H. 1981. Mortality of young black Japanese abalone *Haliotis discus discus* after transplantation. *Bull. Jap. Soc. Sci. Fish.* 47: 151-159.
- KOJIMA, H., Y. NAKAHISA, AND H. TANIMOTO. 1977. A study on the stock of Japanese black abalone, *Haliotis discus discus* in Tokushima Prefecture — I. Growth of shells. *Bull. Tokai Reg. Fish. Res. Lab.* 90: 25-37.
- KOJIMA, H., Y. NAKAHISA, H. TANIMOTO, AND K. ISIBASI. 1978. A study on the stock of Japanese black abalone, *Haliotis discus discus* in Tokushima Prefecture — II. Abalone fishery and its population. *Bull. Tokai Reg. Fish. Res. Lab.* 93: 45-62.
- KOZLOFF, E. N. 1983. Seashore life of the northern Pacific coast. University of Washington, Seattle, WA., 370 p.
- LARSON, R., AND D. BLANKENBECKLER. 1980. Abalone research. Alaska Dep. Fish and Game, Ketchikan, AK., 21 p. (Mimeo)
- LEIGHTON, D. L. 1972. Laboratory observations on the early growth of the abalone, *Haliotis sorenseni*, and the effect of temperature on larval development and settling success. *Fish. Bull.* 70: 373-381.
1974. The influence of temperature on larval and juvenile growth in three species of southern California abalones. *Fish. Bull.* 72: 1137-1145.
- LEIGHTON, D. L., AND R. A. BOOLOOTIAN. 1963. Diet and growth in the black abalone, *Haliotis cracherodii*. *Ecology* 44: 227-238.
- LEIGHTON, D. L., AND C. A. LEWIS. 1982. Experimental hybridization in abalones. *Int. J. Invert. Reprod.* 5: 273-282.
- LESTER, R. J. G. 1986. Abalone die-black caused by protozoan infection? *Aust. Fish.* 45(6): 26-27.
- LEWIS, R. K., S. A. SHEPHERD, P. O'DONOGHUE, AND P. H. PHILLIPS. 1987. Protozoan parasite (*Perkinsus*) infection in abalone: A progress report. *SAFISH* 11(1): 7-8.
- LEWIS, R. K., S. A. SHEPHERD, P. SLUCZANOWSKI, AND G. ROHAN. 1984. An assessment of the South Australian abalone resource. South Australian Department of Fisheries, Adelaide, S. A. 59 p. (Mimeo)
- LEWIS, T. E., C. D. GARLAND, AND T. A. MCMEEKIN. 1985. The bacterial biota on crustose (nonarticulated) coralline algae from Tasmanian waters. *Microb. Ecol.* 11: 221-230.
- LIVINGSTONE, R. 1952. Preliminary investigation of the south-eastern Alaska abalone (*Haliotis kamtschatkana*) Part I — Exploratory diving. *Comm. Fish. Res.* 14: 8-16.
- LOWRY, L. F., AND J. S. PEARSE. 1973. Abalones and sea urchins in an area inhabited by sea otters. *Mar. Biol.* 23: 213-219.
- LUDWIG, D. 1980. Harvest strategies for a randomly fluctuating population. *J. Cons. Int. Explor. Mer* 39: 168-174.
- MCCORMICK, T. B., AND K. O. HAHN. 1983. Japanese abalone culture practices and estimated costs of juvenile production in the U.S.A. *J. World Maricul. Soc.* 14: 149-161.
- MCELDERRY, H., AND L. RICHARDS. 1984. Recreational SCUBA diving in the Strait of Georgia: An analysis of the distribution of diving effort and the importance of collecting marine animals. *Can. MS Rep. Fish. Aquat. Sci.* 1794: 66 p.
- MCLEAN, J. H. 1966. West American prosobranch

- gastropoda: Superfamilies Patellacea, Pleurotomariacea, and Fissurellacea. Ph.D. dissertation, Stanford University, CA. 255 p.
- MC SHANE, P., AND M. SMITH. 1986. Starfish vs abalone in Port Phillip Bay. *Aust. Fish.* 45(6): 16-18.
- MINCHIN, D. 1975. The righting response in *Haliotids*. *Veliger* 17: 249-250.
- MOMMA, H., AND P. SATO. 1969. The locomotion of disc abalone, *Haliotis discus hannai* Ino, and the Siebold's abalone, *Haliotis sieboldi* Reeve, in the fishing grounds. *Tohoku J. Agric. Res.* 20: 150-157.
- MONTGOMERY, D. H. 1967. Responses of two haliotid gastropods (Mollusca), *Haliotis assimilis* and *H. rufescens*, to the forcipulate asteroids (Echinodermata) *Pycnopodia helianthoides* and *Pisaster ochraceus*. *Veliger* 9: 359-368.
- MORRIS, R. H., D. P. ABBOTT, AND E. C. HADERLIE [ed.]. 1980. Intertidal invertebrates of California. Stanford University Press, Stanford, CA. 690 p.
- MORSE, A. N. C., AND D. E. MORSE. 1984. Recruitment and metamorphosis of *Haliotis* larvae induced by molecules uniquely available at the surface of crustose red algae. *J. Exp. Mar. Biol. Ecol.* 75: 191-215.
- MORSE, A. N. C., C. A. FROYD, AND D. E. MORSE. 1984. Molecules from cyanobacteria and red algae that induce larval settlement and metamorphosis in the mollusc *Haliotis rufescens*. *Mar. Biol.* 81: 293-298.
- MORSE, D. E. 1984. Biochemical genetic engineering for improved production of abalones and other valuable molluscs. *Aquaculture* 39: 263-282.
- MORSE, D. E., H. DUNCAN, N. HOOKER, AND A. MORSE. 1977. Hydrogen peroxide induces spawning in mollusks, with activation of prostaglandin endoperoxide synthetase. *Science*, N.Y. 196: 298-300.
- MOTTET, M. G. 1978. A review of the fishery biology of abalones. *Wash. State Dep. Fish. Tech. Rep.* 37: 81 p.
1980. Factors leading to the success of Japanese aquaculture with an emphasis on northern Japan. *Wash. State Dep. Fish. Tech. Rep.* 52: 83 p.
1981. Enhancement of the marine environment for fisheries and aquaculture in Japan. *Wash. State Dep. Fish. Tech. Rep.* 69: 96 p.
- MURRAY, T. E. 1982. Recent trends in the paua fishery, p. 9-13. In J. M. Ackroyd, T. E. Murray, and J. L. Taylor [ed.]. *Proceedings of the Paua Fishery Workshop*. Fish. Res. Div. (N.Z.) Occas. Pub. 41: 43 p.
- NEWMAN, G. G. 1966. Movements of the South African abalone *Haliotis midae*. *S. Africa Div. Sea Fish. Invest. Rep.* 56: 19 p.
1967. Reproduction of the South African abalone *Haliotis midae*. *S. Africa Div. Sea Fish. Invest. Rep.* 64: 24 p.
1968. Growth of the South African abalone *Haliotis midae*. *S. Africa Div. Sea Fish. Invest. Rep.* 67: 24 p.
1969. Distribution of the abalone (*Haliotis midae*) and the effect of temperature on productivity. *S. Africa Div. Sea Fish. Invest. Rep.* 74: 7 p.
- NORMAN-BOUDREAU, K., D. BURNS, C. A. COOKE, AND A. AUSTIN. 1986. A simple technique for detection of feeding in newly metamorphosed abalone. *Aquaculture* 51: 313-317.
- OLSEN, D. 1968. Banding patterns of *Haliotis rufescens* as indicators of botanical and animal succession. *Biol. Bull.* 134: 139-147.
- OLSEN, S. 1984. Shellfish Enhancement Report. NOAA, NMFS, Final Report for Project 1-144-R. Washington State Dep. of Fisheries. 85 p. (Mimeo)
- OWEN, B., J. H. MCLEAN, AND R. J. MEYER. 1971. Hybridization in eastern Pacific abalones (*Haliotis*). *Bull. Los Angeles County Mus. Nat. Hist., Sci.* 9: 37 p.
- PACE, D. 1981. Kelp community development in Barkley Sound, British Columbia following sea urchin removal, p. 457-463. In *Proc. Eighth International Seaweed Symposium*.
- PAINE, R. T. 1986. Benthic community-water column coupling during the 1982-1983 El Niño. Are community changes at high latitudes attributable to cause or coincidence? *Limnol. Oceanogr.* 31: 351-360.
- PAUL, A. J., AND J. M. PAUL. 1981. Temperature and growth of maturing *Haliotis kamschatkana* Jonas. *Veliger* 23: 321-324.
- PAUL, A. J., J. M. PAUL, D. W. WOOD, AND R. A. NEVE. 1977. Observations on food preferences, daily ration requirements and growth of *Haliotis kamschatkana* Jonas in captivity. *Veliger* 19: 303-309.
- PEARSE, J. S. 1978. Reproductive periodicities of Indo-Pacific invertebrates in the Gulf of Suez. IV. The chitons *Acanthopleura haddoni* Winckworth and *Onithochiton lyelli* (Sowerby), and the abalone *Haliotis pustulata* Reeve. *Bull. Mar. Sci.* 28: 92-101.
- PEARSE, P. H. 1982. Turning the tide. A new policy for Canada's Pacific fisheries. Final Report, Commission on Pacific Fisheries Policy. Dep. of Fisheries and Oceans, Vancouver, B.C. 292 p.
- PENG, S. C., K. T. SHAE, AND K. H. CHANG. 1984. Age and growth of small abalone, *Haliotis diversicolor supertexta* (Lischke), in Hualien, Taiwan. *Bull. Inst. Zool., Academia Sinica* 23: 29-38.
- PETERSON, C. H. 1983. A concept of quantitative reproductive senility: application to the hard clam, *Mercenaria mercenaria* (L.)? *Oecologia (Berl.)* 58: 164-168.
- POORE, G. C. B. 1972a. Ecology of New Zealand abalones, *Haliotis* species (Mollusca:Gastropoda) 2. Seasonal and diurnal movement. *N.Z. J. Mar. Freshwat. Res.* 6: 246-258.
- 1972b. Ecology of New Zealand abalones, *Haliotis* species (Mollusca:Gastropoda) 3. Growth. *N.Z. J. Mar. Freshwat. Res.* 6: 534-559.
- 1972c. Ecology of New Zealand abalones, *Haliotis* species (Mollusca:Gastropoda) 1. Feeding. *N.Z. J. Mar. Freshwat. Res.* 6: 11-22.
1973. Ecology of New Zealand abalones, *Haliotis* species (Mollusca:Gastropoda) 4. Reproduction. *N.Z. J. Mar. Freshwat. Res.* 7: 67-84.
- PRINCE, J. D., AND W. B. FORD. 1985. Use of anaesthetic to standardize efficiency in sampling abalone populations (Genus *Haliotis*; Mollusca: Gastropoda). *Aust. J. Mar. Freshwat. Res.* 36: 701-706.
- PRINCE, J. D., T. L. SELLERS, W. B. FORD, AND S. R. TALBOT. 1987. Experimental evidence for limited dispersal of haliotid larvae (genus *Haliotis*; Mollusca: Gastropoda). *J. Exp. Mar. Biol. Ecol.* 106: 243-263.
- QUAYLE, D. B. 1962. Abalones in British Columbia. *Progress Rep. Pacific Coast Station No.* 114: 9-12.
1971. Growth, morphometry and breeding in the British Columbia abalone (*Haliotis kamschatkana* Jonas). *Fish. Res. Board Can. Tech. Rep.* 279: 84 p.
- RICKER, W. E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.* 191: 382 p.
- RICKETTS, E. F., J. CALVIN, J. W. HEDGEPEETH, AND D. W. PHILLIPS. 1985. *Between Pacific tides*. (5th Ed.) Stanford University Press, Stanford, CA., 625 p.
- SAINSBURY, K. J. 1977. Population dynamics and fishery management of the abalone, *Haliotis iris*. Ph.D. Thesis, Univ. of Canterbury, Christchurch, N.Z. 183 p.
1980. The effects of individual variation on the von Bertalanffy growth equation. *Can. J. Fish. Aquat. Sci.* 37: 241-247.

- 1982a. Population dynamics and fishery management of the paua, *Haliotis iris*. 1. Population structure, growth, reproduction, and mortality. N.Z. J. Mar. Freshwat. Res. 16: 147-161.
- 1982b. Population dynamics and fishery management of the paua, *Haliotis iris*. 2. Dynamics and management as examined using a size class population model. N.Z. J. Mar. Freshwat. Res. 16: 163-173.
- SAITO, K. 1981. The appearance and growth of 0-year Ezo abalone. Bull. Jap. Soc. Sci. Fish. 47: 1393-1400.
1984. Ocean ranching of abalones and scallops in northern Japan. Aquaculture 39: 361-373.
- SAKAI, S. 1960. On the formation of the annual ring on the shell of the abalone, *Haliotis discus* var. *hannai* Ito. Tohoku J. Agric. Res. 11: 239-244.
1962. Ecological studies on the abalone, *Haliotis discus hannai* Ito-IV. Studies on the growth. Bull. Jap. Soc. Sci. Fish. 28(9): 899-904.
- SCHAEFER, M. B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Inter-Am. Trop. Tuna Comm. Bull. 1: 25-56.
- SCHNUTE, J., AND D. A. FOURNIER. 1980. A new approach to length-frequency analysis: Growth structure. Can. J. Fish. Aquat. Sci. 37: 1337-1351.
- SEKI, T., AND H. KANNO. 1977. Synchronized control of early life in the abalone, *Haliotis discus hannai* Ito (Haliotidae, Gastropoda). Bull. Tohoku Reg. Fish. Res. Lab. 38: 143-153.
1981. [Induced settlement of the Japanese abalone, *Haliotis discus hannai*, veliger by the mucous trails of the juvenile and adult abalones.] Bull. Tohoku Reg. Fish. Res. Lab. 43: 29-36. (Transl. from Japanese by Can. Transl. Fish. Aquat. Sci. No. 4876, 1982.)
- SHEPHERD, S. A. 1973a. Studies on Southern Australian abalone (genus *Haliotis*). I. Ecology of five sympatric species. Aust. J. Mar. Freshwater Res. 24: 217-257.
- 1973b. Competition between sea urchins and abalone. Aust. Fish. 32(6): 4-7.
1975. Distribution, habitat and feeding habits of abalone. Aust. Fish. 34(1): 1-4.
- 1986a. Studies on Southern Australian abalone (genus *Haliotis*). VII. Aggregative behaviour of *H. laevis* in relation to spawning. Mar. Biol. 92: 231-236.
- 1986b. Movement of the Southern Australian abalone *Haliotis laevis* in relation to crevice abundance. Aust. J. Ecol. 11: 295-302.
- SHEPHERD, S. A., P. S. CLARKSON, AND J. A. TURNER. 1985. Studies on Southern Australian abalone (genus *Haliotis*). V. Spawning, settlement and early growth of *H. scalaris*. Trans. R. Soc. S. Aust. 109: 61-62.
- SHEPHERD, S. A., AND W. S. HEARN. 1983. Studies on Southern Australian abalone (genus *Haliotis*). IV. Growth of *H. laevis* and *H. ruber*. Aust. J. Mar. Freshwater Res. 34: 461-475.
- SHEPHERD, S. A., G. R. KIRKWOOD, AND R. L. SANDLAND. 1982. Studies on Southern Australian abalone (genus *Haliotis*). III. Mortality of two exploited species. Aust. J. Mar. Freshwat. Res. 33: 265-272.
- SHEPHERD, S. A., AND H. M. LAWS. 1974. Studies on Southern Australian abalone. II. Reproduction of five species. Aust. J. Mar. Freshwater Res. 25: 49-62.
- SHEPHERD, S. A., AND J. A. TURNER. 1985. Studies on Southern Australian abalone (genus *Haliotis*). VI. Habitat preference, abundance and predators of juveniles. J. Exp. Mar. Biol. Ecol. 93: 285-298.
- SLOAN, N. A., AND S. FARLINGER. 1987. Abalone, p. 63-67. In G. S. Jamieson and R. M. Harbo [ed.]. 1986 Shellfish management advice, Pacific Region. Can. MS Rep. Fish. Aquat. Sci. 1756.
- SLUCZANOWSKI, P. R. 1984. A management oriented model of an abalone fishery whose substocks are subject to pulse fishing. Can. J. Fish. Aquat. Sci. 41: 1008-1014.
1986. A disaggregate model for sedentary stocks: The case of South Australian abalone, p. 393-401. In G. S. Jamieson and N. Bourne [ed.]. North Pacific workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.
- SMITH, S. V. 1972. Production of calcium carbonate on the mainland shelf of southern California. Limnol. Oceanogr. 17: 28-41.
- SPROUT, P. E. 1983. Review of 1981 commercial abalone fishery in British Columbia. Can. MS Rep. Fish. Aquat. Sci. 1692: 23 p.
- SENTONGO, G. W., AND P. A. LARKIN. 1973. Some simple methods of estimating mortality rates of exploited fish populations. J. Fish. Res. Board Can. 30: 695-698.
- STENECK, R. S. 1986. The ecology of coralline algal crusts: Convergent patterns and adaptive strategies. Ann. Rev. Ecol. Syst. 17: 273-303.
- STEPHENSON, T. A. 1924. Notes on *Haliotis tuberculata*. I. J. Mar. Biol. Assoc. U. K. 13: 480-495.
- STEWART, E. A., J. B. FOSTER, J. A. CARSON, AND P. A. BREEN. 1982. Observations of sea urchins, other invertebrates and algae in an area inhabited by sea otters. Can. MS Rep. Fish. Aquat. Sci. 1655: 28 p.
- TALMADGE, R. R. 1977. Notes on a California hybrid *Haliotis* (Gastropoda: Haliotidae). Veliger 20(1): 37-38.
- TANAKA, K., O. ISHIDA, AND T. TANAKA. 1986a. On the bottom features and current of nursery ground of abalone at the southern coast of Chiba Prefecture. Bull. Jap. Soc. Sci. Fish. 52: 1515-1523.
- TANAKA, K., T. TANAKA, O. ISHIDA, AND T. OHBA. 1986b. On the distribution of swimming and deposited larvae of nursery ground of abalone at the southern coast of Chiba Prefecture. Bull. Jap. Soc. Sci. Fish. 52: 1525-1532.
- TANAKA, K., O. ISHIDA, AND T. TANAKA. 1986c. On the lost weight of abalone around Mera Shoal in the southern coast of the Boso Peninsula, Japan. I. On the distribution of abalone. Bull. Japan Sea Reg. Fish. Res. Lab. 36: 49-58.
- TEGNER, M. J. 1980. Multispecies considerations of resource management in southern California kelp beds. Can. Tech. Rep. Fish. Aquat. Sci. 954: 125-143.
1988. The California abalone fishery: production, ecological interactions, and prospects for the future. In J. F. Caddy [ed.]. Scientific approaches to management of shellfish resources. J. Wiley and Sons, New York, NY.
- TEGNER, M. J., AND R. A. BUTLER. 1985a. Drift-tube study of the dispersal potential of green abalone (*Haliotis fulgens*) larvae in the southern California Bight: implications for recovery of depleted populations. Mar. Ecol. Prog. Ser. 26: 73-84.
- 1985b. The survival and mortality of seeded and native red abalones, *Haliotis rufescens*, on the Palos Verdes Peninsula. Calif. Fish Game 71: 150-163.
- TEGNER, M. J., AND P. K. DAYTON. 1987. El Niño effects on southern California kelp forest communities. Adv. Ecol. Res. 17: 243-279.
- TEGNER, M. J., P. A. BREEN, AND C. E. LENNERT. 1988. Population biology of red abalones (*Haliotis rufescens*) in southern California and management of the red and pink (*H. corrugata*) fisheries.
- TEGNER, M. AND L. A. LEVIN. 1982. Do sea urchins and abalones compete in California kelp forest communities?, p. 265-271. In J. M. Lawrence [ed.]. Proc. Int. Echinoderm Conf., Tampa Bay. A. A. Balkema, Rotterdam.
- THOMPSON, W. F. 1914. Report on the abalones of British

- Columbia (*Haliotis gigantea*, Chemnitz). [= *H. kamtschakana* Jonas] Rep. B.C. Commissioner Fish. (1913), 126-130.
- THOMSON, R. E. 1981. Oceanography of the British Columbia coast. Can. Spec. Publ. Fish. Aquat. Sci. 56: 291 p.
- TUTSHULTE, T. C. 1973. The comparative ecology of three sympatric abalones. PhD. thesis, University of California, San Diego, CA. 355 p.
- UKI, N. 1984. Abalone culture in Japan. NOAA, N.M.F.S. Tech. Rep. 16: 83-88.
- UKI, N., AND S. KIKUCHI. 1984. Regulation of spawning of an abalone, *Haliotis* (Gastropoda) by external environmental factors. Aquaculture 39: 247-261.
- URSIN, E. 1967. A mathematical model of fish growth. J. Fish. Res. Board Can. 24: 2355-2453.
- VAN SICKLE, J. 1977. Mortality rates from size distributions. Oecologia 27: 311-318.
- VASSEROT, J. 1983. Perspective d'accroissement de la production mondiale d'ormeaux par l'extension des aires géographiques peuplées de mollusques comestibles de la famille de Haliotides, grâce à l'introduction d'espèces appropriées dans la zone littorales actuellement dépourvues de ces gastéropodes. J. Rech. Oceanogr. 8: 23-33.
- VOLTZOW, J. 1983. Flow through and around the abalone *Haliotis kamtschakana*. Veliger 26: 18-21.
1986. Changes in pedal intramuscular pressure corresponding to behaviour and locomotion in the marine gastropods *Busycon contrarium* and *Haliotis kamtschakana*. Can. J. Zool. 64: 2288-2293.
- WALTERS, C. J. 1975. Optimal harvest strategies in relation to environmental variability and uncertainty about production parameters. J. Fish. Res. Board Can. 32: 1777-1784.
- WITHERSPOON, N. B. 1975. Sizes in the Tasmanian commercial catch of black-lip abalone (*Haliotis ruber*) — possible effects of changing habitat during growth. Tasmanian Fish. Res. 9(1): 15-22.
- WRIGHT, M. B. 1975. Growth in the black abalone, *Haliotis cracherodii*. Veliger 18: 194-199.
- YANO, I. AND Y. OGAWA. 1977. Effects of light, temperature and hydrostatic pressure on vertical distribution of abalone larvae. *Haliotis gigantea*. Bull. Tokai Reg. Fish. Res. Lab. 91: 1-12.
- YOUNG, J. S. AND J. D. DEMARTINI. 1970. The reproductive cycle, gonadal histology, and gametogenesis of the red abalone, *Haliotis rufescens* (Swainson). Calif. Fish Game 56: 298-309.
- ZIMMERMAN, R. C. AND D. L. ROBERTSON. 1985. Effects of El Niño on local hydrography and growth of the giant kelp, *Macrocystis pyrifera*, at Santa Catalina Island, California. Limnol. Oceanogr. 30: 1298-1302.